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Phylogenetic Significance of Blood Proteins among Some Orthopteroid Insects[1]

W. P. STEPHEN

THE SPECIES specificity of blood protein fractions and the use of these patterns as indicators of relationship between and among different vertebrate taxa has been reported or suggested by several authors (Deutsch and Goodloe, 1945; Dessauer and Fox, 1956; Johnson and Wicks, 1959). These papers have dealt primarily with investigations of the value of protein patterns by paper electrophoresis in separating various taxa. More recently Zweig and Crenshaw (1957) and Dessauer and Fox (1956, 1958) have shown that geographical races of turtles, snakes, and some amphibians can be differentiated by quantitative and qualitative differences in their plasma protein patterns.

The potential value of this technique as an objective method of differentiating between and among species has been mentioned by several of the above authors. While the objectivity is not absolute in that further extrapolation of the data is necessary, it precludes the somewhat arbitrary selection of "significant" morphological characteristics on which relationship is based.

The studies that have been conducted on the blood protein fractions of insects are for the most part restricted to a few individuals representing distantly related taxa. Electrophoretic separation of insect blood protein fractions has indicated the potential value of this tool in entomological systematics (Clark and Ball, 1957; Stephen and Steinhauer, 1957; Stephen, 1958; Brezner and Enns, 1959). The small size and limited amount of blood available from an individual insect has necessitated a deviation from the conventional pretreatments accorded vertebrate blood. The quantities of blood available from most vertebrates permit plasma separation and dialysis of each blood specimen prior to electrophoresis. In insects, however, a compromise must be made. Either large series of blood samples can be pooled and accorded a stabilizing pretreatment, or individual whole "blood" samples can be subjected to immediate separation. The former of the alternatives results in a mean protein analysis while the latter is necessary to secure information on individual variation as well as on the variation among and between individuals of different populations. The magnitude of protein fraction variability among individuals from a single population suggests that replicated series of a number of specimens from each phyletic unit are necessary to determine the validity of conclusions on phylogenetic relations that are to be drawn from blood protein analyses. Distinct quantitative and qualitative differences in proteins have been found to exist between the sexes of the same species; more striking changes in the protein patterns were noted between the immatures and the imagos among the holometabolous forms of the same species of insect (Stephen and Steinhauer, 1957). In addition, changes in the relative concentrations of various proteins as well as the appearance and disappearance of supplementary fractions have been noted to occur during the development of hemimetabolous forms (Steinhauer and Ste-

[1] Technical Paper No. 1341, Oregon Agricultural Experiment Station.

phen, 1959). With these established sources of variation in the blood proteins of a single population it becomes apparent that care must be exercised in the selection of specimens to be utilized in comparative protein studies between and among species, and that some knowledge of the development is necessary to validate any conclusions drawn from the electropherograms.

This paper presents the data obtained from a study of the blood protein fractions of 19 species of orthopteroid insects to determine their possible contributions to a better understanding of the relationship between and among various insect species. Principal attention is directed at the protein analyses of 14 species representing 11 different genera of cockroaches in which stringent selection for uniformity of environmental conditions and chronological age could be met. Several other orthopteroid species were sampled to determine the degree of similarity among the blood proteins of the various species in different families of the same order.

Methods

The following species were selected for this study: the roaches, *Blaberus craniifer* Burm.; *B. giganteus* (L.); *Blatta orientalis* L.; *Blattella germanica* (L.); *Cryptocercus punctulatus* Scudder; *Diploptera dytiscoides* (Serville); *Eurycotis floridana* (Walker); *Leucophaea maderae* (Fabr.); *Nauphoeta cinerea* (Oliver); *Neostylopyga rhombifolia* (Stoll); *Parcoblatta americana* (Scudder); *Periplaneta americana* (L.); *P. australasiae* Fabr.; *P. brunnea* Burm.; the two lined grasshopper, *Melanoplus bivittatus* (Say); the lubber, *Brachystola magna* (Scudder); the mantid, *Paratenodera sinensis* (Sauss.); the field cricket, *Acheta assimilis* (Fabr.); and the camel cricket, *Ceuthophilus* sp.

The 14 species of roaches have been maintained in culture at Oregon State College from three to five years. Each of the 14 species has been fed on identical diets and housed in the same quarters. Because of the marked qualitative as well as the quantitative differences in blood proteins between the sexes, only the females were used in comparative analysis. With the exception of *Blaberus giganteus,* a minimum of 20 specimens was sampled and analyzed in duplicate, triplicate, or quadruplicate during the course of the studies (the extent of replication was determined by total blood supply of the individual). Only four specimens of *B. giganteus* were available to the author, and these four were sampled as late instar nymphs and again as adults. The adult blood samples from each individual were replicated from five to eight times.

The non-roach specimens in this study were secured from the field and maintained under laboratory conditions until their death. Of these species only the field cricket, *Acheta assimilis,* was adaptable to laboratory culture. With this species the same stringent controls in the selection of the individuals for analysis were made.

All "blood" samples were taken by means of a direct heart puncture through the intersegmental membrane on the abdominal dorsum. Full series aliquots of 10 lambda of whole blood were applied directly to the paper electrophoresis system for analysis. Duplicate or triplicate runs of the same specimen were conducted in each of the two cells. A sample of blood from the roach *P. americana* was included in each cell as a standard of reference on fraction mobility. Previous studies have shown that a supplemental blood protein fraction is found in the nymph and adult of *P. americana,* which appears to be closely associated with the molting processes. If similar protein fractions are found to be common to hemimetabolous forms, and if these particular proteins are genetically determined, then it was felt that they may also contribute to an understanding of the relationships between and among the species. Thus both nymphal and mature adult specimens from all of the roaches except *Parcoblatta*

americana were sampled for blood protein determination. Nymphs of the mantid and the camel cricket were not available during the period in which the study was conducted.

Protein separation was conducted on a Durrum type hanging-strip cell as manufactured by Spinco Division of Beckman instruments. The standard methods of analyses were employed throughout the series of studies (Beckman Bulletin ORI-1; Beckman Bulletin RIM-5). In method A the veronal buffer with an ionic strength of 0.05 and a pH of 8.6 was used as the solvent system and the blood samples were applied to paper strips of Whatman 3 mm. paper. The blood proteins were separated by running each cell at a current of 5 ma. for a period of 16 hours. In method B a veronal buffer was again used but with an ionic strength of 0.075 and a pH of 8.6, and the proteins separated on strips of S and S 2043-A paper.

The electropherograms obtained by method A were set aside for 24 hours to permit color oxidation and then scanned using the Spinco Analytrol R A. The electropherograms obtained from method B were set aside for 3 days and then placed in a saturated atmosphere of ammonium hydroxide for 15 minutes prior to the scanning with the Analytrol model R B.

Comparisons of the electropherograms and the scans were made to determine the fractions and their mobilities in each system. As in previous studies the intensely colored point of application was not included in the computation of specific proteins nor was the stain intensity considered in the total protein concentrations. The application point is believed to consist in part of melanin which oxidizes upon exposure to the atmosphere (Stephen, 1958).

The protein fractions are labeled on the basis of their mobility in millimeters from the point of application in a given buffer system, at a given current, and on a given paper. It should be emphasized that each peak may represent one or more protein fractions that have migrated at a similar rate of speed and that the absence of a given fraction may mean that it is present in such trace amounts that the method employed does not permit its identification. The data on the fractions isolated from each species are presented in Table 1. Their recorded mobility is based on the data secured from Method A procedures in analysis. Fractions found only in the mature forms are indicated by an "X," and the developmentally-associated protein fractions by an "N." The relative concentrations of the various protein fractions are not included in the table because of the considerable fluctuation each fraction undergoes during development, and because it was felt that this phase of the data was incidental to the main treatise.

Results and Discussion

Only the data on mobility of each protein fraction as obtained under Method A are presented in Table 1. The analysis of mobility and concentrations of the fractions using Method B indicated no quantitative nor qualitative differences between and among the various components when compared with Method A. The blood of the mature adults of the cockroach species sampled yielded two protein fractions. An additional fraction (the developmentally-associated fraction) was found in the nymphal and early adult stages of the species of *Blaberus, Blatta, Eurycotis, Leucophaea, Nauphoeta, Neostylopyga,* and *Periplaneta.* It is noteworthy, however, that the consistency with which these fractions appeared during development was considerably different from that of *Periplaneta americana.* As indicated in a previous paper (Steinhauer and Stephen, 1959) the supplementary fraction associated with nymphal development was found to be present during all of the preadult stages except for a very brief period during the middle of each stadium. Similar observations on the developmentally-associated protein fractions were found with *P. brunnea* and *P. australasiae.* However, only 70% of the nymphs of the other

TABLE 1—Protein fractions recorded from the blood of females of 19 species of orthopteroid insects. Fractions found in the adults are recorded with an "X," those that occur only in the nymph by an "N." The motility is recorded in mm. from the point of application (O).

SPECIES	−18±3	−7±3	0	10±3	16±3	26±3	36±3	58±3
Cryptocercus				X		X	N?	
Diploptera				X		X	N?	
Blatta				X		N	X	
P. americana				X		N	X	
P. australasiae				X		N	X	
P. brunnea				X		N	X	
Eurycotis				X		N	X	
Neostylopyga				X		N	X	
Blattella				X	N?		X	
Parcoblatta				X			X	
Leucophaea				N		X	X	
Nauphoeta				N		X	X	
B. craniifer				N			X	X
B. giganteus				N			X	X
Paratenodera					X	X		X
Melanoplus		N		X		X		
Brachystola		N			X	X		
Acheta	X	N			X	X		
Ceutophilus				X	X			

species mentioned immediately above yielded what the author considers to be developmentally-associated protein fractions with mobilities differing from those fractions common to the imagos. The reasons for these intergeneric differences may be manifold, and it is considered that this phase of the investigation lies beyond the scope of the present paper. Throughout the series of several hundred replicates run on the species of the above genera, the mobility of the nymphal fraction was completely replicable and characteristic for each species.

The replicates of the nymphal blood samples from *Diploptera dytiscoides*, *Cryptocercus punctulatus*, and *Blattella germanica* did not yield the supplementary fraction with a consistency common to the other species in the study. This may mean: that such fractions do not occur in the species; that these fractions are present in such small quantities that the method does not permit their detection; or that the period of the nymphal stadium during which they are present is of very short duration. The latter two hypotheses appear to be the most probable, for traces of supplementary nymphal fractions have been noted from isolated specimens of all three species. The paucity of data on the nymphal fractions from these species makes their positive identification impossible. A tentative identification of the nymphal fractions of these three species is indicated in Table 1 followed by a question mark.

A total of five different protein fractions ranging in mobility from 10±3 to 58±3 mm. from the point of application were found among the 14 roach species run. Fractions 10±3 and 36±3 were present in all of the roach species either as adult or nymphal proteins. Fraction 26±3 was not taken from the nymps or adults of *Blattella*, *Parcoblatta* or the two species of *Blaberus*. Fraction 58±3 was specific to the adults of the genus *Blaberus*, and fraction 16±3 has been tentatively identified from the blood of two nymphs of *Blattella germanica*.

One or more of five protein fractions was recorded from the five other orthopteroid species on which blood analysis was conducted. These ranged from the negatively migrating fractions at minus 18±3 to 26±3. Only in the field cricket, *Acheta assimilis*, and in *Paratenodera* were more than two fractions recorded in the mature adult. It is interesting to

note that in both species of grasshopper, as well as in the field cricket, there occurred negatively migrating fractions not found among any of the roaches sampled. There was little similarity in the blood protein fractions between five orthopteroid species and any of the roaches in the study.

Eight of the cockroach species have the two fractions, 10±3 and 36±3, in common in the adult stage. If judgment on the relationship were to be made solely on the blood protein fractions, these species could be considered as a distinct phyletic unit. The tentative determination of a nymphal fraction at 16±3 in *Blattella*, and its presumed presence in *Parcoblatta*, would separate these two species from the remaining six. The similarity of the blood protein fractions in the mature females permits a ready separation of three distinct groups in addition to the one mentioned above: *Cryptocercus* and *Diploptera* with the fractions 10±3 and 26±3 in common; *Nauphoeta* and *Leucophaea* with the fractions 26±3 and 36±3; and the two species of *Blaberus* with fractions 36±3 and 58±3.

Consideration of the protein fractions associated with development strengthens these group associations. In each of the species (with the possible exception of the tentatively questioned nymphal fractions in Table 1), the nymphal fraction has a mobility unique to the group in which it is included.

It should be noted that marked quantitative differences are found to occur between and among the protein fractions common to each of the species of roaches, and these differences appear to be stable through most of the adult life of each organism. As indicated in a previous paper (Stephen, 1958) these quantitative differences are often of a sufficient magnitude to permit species separation. Species separation on this basis is impossible among the species of *Periplaneta*. In other genera, however, subtle specific differences in blood patterns are obtainable if the separation is conducted under closely controlled conditions.

This technique of species discrimination is not intended to offer a replacement for the conventional method of morphological determination of relationship among the different taxa. It is, however, an indication that blood protein fractions may present a valuable supplementary tool for the objective evaluation of relationship between and among various organisms. The blood or circulating hemolymph of any organism appears to be a character which undergoes a slow evolutionary change. This is not meant to imply that the blood is the most primitive characteristic in any or all organisms, but merely that the blood can be considered as one of the more stable genotypic characters within a phyletic line of descent. There are considerable data, particularly from the mammals and other higher vertebrates, supporting the conclusions that specific, generic, and even ordinal blood protein patterns are qualitatively similar.

Since this study is intended to be a preliminary appraisal of the blood protein characteristics in determining relationships among insects, it is interesting to compare the specific and generic groupings obtained with one of the conventional revisionary treatments of the roaches. Rehn (1951) considers the genera included in this study as members of three distinct families: Diplopteridae (*Diploptera*); Panesthiidae (*Cryptocercus*); and Blattidae which includes the remaining species in four subfamilies (Table 2A). As indicated above, the species sampled in this study fall into four distinct groups on the basis of their protein constituents (Table 2B). The similarity in blood protein fractions (10±3 and 26±3) between *Cryptocercus* and *Diploptera* is here interpreted as indicating that these two genera should be included in the same taxon (Group I). These two genera are considered to compose the first and most primitive group of roaches sampled for this study. "Primitiveness" is here based on comparative morphology and habits.

TABLE 2—Comparative classifications of some cockroaches based on morphology and blood proteins.

A. MORPHOLOGICAL CLASSIFICATION (AFTER REHN, 1951)		B. BLOOD PROTEIN CLASSIFICATION		
Diplopteridae	*Diploptera*	Supergroup I		
Panesthiidae	*Cryptocercus*	Group 1		*Diploptera*
Blattidae				*Cryptocercus*
Blattinae	*Blatta*	Group 2		
	Eurycotis		Subgroup A	
	Neostylopyga			*Blatta*
	Periplaneta			*Eurycotis*
Epilamprinae				*Neostylopyga*
Leucophaeini				*Periplaneta*
	Leucophaea		Subgroup B	
Nauphoetini				*Parcoblatta*
	Nauphoeta			*Blattella*
Blaberinae	*Blaberus*	Supergroup II		
Pseudomopinae		Group 3		*Leucophaea*
Parcoblattini				*Nauphoeta*
	Parcoblatta	Group 4		*Blaberus*
Blattellini				
	Blattella			

Group II is composed of the genera *Periplaneta, Blatta, Neostylopyga, Eurycotis, Blattella,* and *Parcoblatta,* all having the fraction 10±3 and 36±3 common to the mature adults. This group is divided into two subgroups on the basis of the tentative identification of differences in the nymphal fractions between *Blattella* and the species of the first four genera mentioned above. With the absence of the nymphal samples of *Parcoblatta,* this genus is included with *Blattella* in this subgrouping on the basis of morphological and behavioral characteristics. The species of Subgroup A resemble those of Group I in having the same three fractions present in the composite nymphal and adult samples. Subgroup B lacks the fractions 26±3 in either nymphal or adult blood, and is hence considered to be more remote from Group I than Subgroup A. Rehn also considers the genera *Blattella* and *Parcoblatta* to be sufficiently distinct from the Blattinae (Subgroup A) to merit subfamily status.

Group III, consisting of the genera *Leucophaea* and *Nauphoeta,* differs rather markedly from the previous generic groupings. The absence of fraction 10±3, common to the adults of all of the previous species, indicates a divergence of a magnitude warranting full group status. The presence of fraction 10±3 in the nymphs and the fractions 26±3 and 36±3 in the adult are interpreted as indicating its possible derivation from Group I or Group II Subgroup A. Considering the comparative morphology and habits, the latter association would appear to be most probable. Rehn treats these two genera as members of two tribes of the subfamily Epilamprinae of the Blattidae.

The fourth group, as here interpreted, includes the two species of *Blaberus* which lack both fractions 10±3 and 26±3 in the mature adults and have the strikingly unique fraction at 58±3. As this is the only included genus having a fraction of a mobility of this magnitude among the roaches, it is considered to be a highly divergent form meriting full group status. The presence of the fractions 10±3 in the nymphal blood, plus the mutual occurrence of 36±3 in the adults tends to indicate a close affinity between Group III and Group IV. As in the previous group Rehn considers the species of *Blaberus* to constitute a subfamily of the Blattidae.

A further perusal of the electrophoretic data indicates that 14 roach species can be separated into two distinct higher categories, Supergroups A and B. These su-

pergroupings are based on blood characteristics unique to each, and supported by certain biological criteria. Supergroup I is characterized by having fraction 10±3 common to all of the mature adults; in having the blood relatively free flowing with a tendency to form only weak clots on exposure; and in reproducing through the deposition of egg cases. Supergroup II lacks the fraction 10±3 in the mature adults, has blood which forms a very dense, gelatinous coagulum on exposure to oxygen, and its members give birth to living young.

It is evident that the interpretation of relationships based on the blood protein fractions in the roaches is in relatively close accord with the morphological revision at genus-group level. Beyond this, however, the interpretations of the higher taxa differ markedly. Whether these taxa be given family or ordinal status is purely a subjective matter left to the discretion of the revisor. The important point, and ultimate goal of the systematist in erecting the higher categories of any phyletic unit, is that each of the subjective delineations be separated by gaps of approximately equal magnitude. Although these studies are based on a meager sample of the total number of described roach species, they do indicate that the blood proteins may provide us with a yardstick by which these gaps may be more accurately measured.

The conclusion of Dessauer et al. (1957) that electrophoretic mobilities become more rewarding in comparing lower taxonomic units, may apply to the amphibians, reptiles, or mammals that are represented by comparatively few species. In insects, however, with the multitude of closely related species occupying comparatively restricted ecological niches, the similarities among the plasma proteins are more obvious and differences at the specific level much more subtle.

There are several factors that restrict the general application of this technique to entomological systematics. The most apparent of these is associated with the extent of protein variability of the individual during its development. As indicated in the text, the pattern of the developmentally-associated proteins of the roaches varies from group to group, and with the meager data at hand it is impossible to predict at what period of the stadium such fractions should be discernible. The differences in the blood proteins between the immatures and the imagos are even more pronounced in the holometabolous insects where distinct qualitative changes are noted to occur. Contrasting with the Hemimetabola, there is no evidence of an accessory fraction associated with the larval molts in Holometabola (Stephen, unpublished data).

Reports of qualitative and quantitative differences in protein fractions of the blood have been noted among different geographical races of snakes, and fish, which would indicate that similar variation could be expected from the blood of polytypic insect species. Analyses of several populations of *P. americana* and *B. germanica* have failed to yield significant replicable differences that could be ascribed to spatial separation. This is not surprising since the roaches are a remarkably monotypic group whose species are readily amenable to human transport. With the absence of any analytical data on the blood of the highly polymorphic or polytypic forms, the extent of protein variability is conjectural.

There are indications of other sources of blood protein variation in insects but the cause and the extent of this variability is yet to be determined. It is interesting to note some of the sources of variation in blood proteins that have been reported from the warm-blooded vertebrates including man. That no direct extrapolation of the type or magnitude of change can be made to investigations in insects is an indication that the causes of protein variability may be multitudinous. There are numerous reports that the onset of a physiological disturbance (Ericson,

Clegg, and Hein, 1955; Young and Webber, 1953), the incidence of parasitism (Leland, Lindquist, and Lillevik, 1955), or merely a nonpathological, congenital anomaly (Bernfeld, Donahue, and Homburger, 1953), may precipitate qualitative and/or quantitative differences in vertebrate globulins and albumins. It would thus appear essential that large series of specimens be sampled prior to the formulation of any conclusion based on comparative fraction mobility, or that the causes of variability be thoroughly understood. A stringent control over the selection of material to be analyzed becomes a necessity, but achieving these central conditions for most species is often highly impractical.

The technique, particularly in insects, does not present a panacea for the solution of all specific or phylogenetic problems, but rather will have a limited application to the better represented groups in which live material is readily available.

Summary

1. Five different protein fractions were recorded from the blood of the 14 species of cockroaches analyzed, and these fractions were found to be replicable and characteristic for each species. Two additional fractions were recorded from the blood of the other orthopteroid species run and the patterns from these species were distinct from any of the cockroaches used in the study.

2. The cockroaches are grouped on the basis of the similarity of blood protein patterns on the electropherograms. Relationships are in close accord with the morphological conclusions at the genus-group level, but the interpretation of the higher taxa is markedly different.

3. In the cockroaches, the value of blood protein separation as a systematic supplement, appears to be of less value in infraspecific discrimination than reported for various vertebrate taxa.

4. Sources of qualitative and quantitative variation in insect blood proteins are indicated and stringent control over the selection of material to be analyzed is deemed necessary.

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The Influence of Vertical Migration on Speciation in the Oceanic Plankton

P. M. DAVID

Introduction

IT HAS been pointed out that although there is about three hundred times more space for life to exist in the oceans than there is on land, the number of marine species is less than one-fifth of the total recorded in the world (Hesse, Allee, and Schmidt, 1951). However about three-quarters of the terrestrial total is made up by insects, a group which is virtually absent from the marine fauna, and, as Hutchinson (1959) suggested, if this group is disregarded the marine fauna would seem to be the more diverse. The marine environment is particularly remarkable for its uniformity and for the apparent absence of isolating barriers and it is these features which are usually regarded as the explanation of the small numbers of species recorded from that environment. Of the major divisions of the oceanic environment the littoral fauna inhabits a narrow rim around the ocean, the benthic fauna a layer perhaps only a few centimeters thick on the floor of the oceans, while the greatest volume is the province of the oceanic plankton and nekton; this province is the most uniform part of the marine environment and yet the diversity of its fauna is remarkable.

The Planktonic Environment

Variations in temperature and salinity in the oceans occur over a range of 32°C and 7‰ respectively (that is if parts of the Red Sea and areas of melting ice are disregarded), and the other chemical constituents of the oceans vary through similarly small ranges. The environment is a continuous one and a species which could tolerate the range of physical and chemical conditions mentioned would find no barrier to its spread throughout all the oceans. With a somewhat reduced tolerance a species might be restricted to either the Atlantic or the Indo-Pacific regions by the isolating effect first of South America and then of Africa, but in fact geographic features so important in the evolution of the land fauna play a much less important part in dividing up the oceanic environment though of course they are to some extent effective in dividing the benthic regions (Ekman 1953; 286 et seq.).

The main divisions found in the oceans are the boundaries between water masses. A water mass may be described for the purpose of this paper as a large circumscribed body of water which has characteristic physical and chemical features and which is separated from other water masses by more or less narrow boundary regions where the physical and chemical characteristics of the water alter comparatively abruptly. At present about eighteen such water masses are distinguished (Sverdrup, Johnston, and Fleming, 1942: 605 et seq.).

Not all the boundaries between water masses have been shown to be boundaries to the spread of animals, but a large body of evidence is building up to show that a number of these physical and chemical boundaries are faunistic boundaries also (John, 1936; David, 1955; Tebble, 1960), and even the species which are distributed in several water masses may well prove in many cases to be represented in each water mass by a local race or popu-

lation largely confined to it (David, 1955). It is not difficult to imagine that regions of mixed water where abrupt and large changes of physical and chemical conditions occur, which are now effective as faunistic boundaries, have been effective in the past in the evolution of new forms.

This simple hypothesis coupled with a more sophisticated one advanced by Brinton (1959) may well explain the evolution of at least part of the planktonic fauna, but the diversity of species so often found at one spot in the ocean seems to suggest that other mechanisms must also have been at work.

Perhaps one of the most remarkable published instances of this diversity is to be found in the reports of the Carnegie Expedition: Wilson (1942) records that at Station 56 (31°49′S, 109°04′W) 108 species of planktonic copepods were taken between the surface and 100 meters. Certainly some of these species have since been found to be synonymous and the recorded number of species is too high, but even so the total is most remarkable, and one feels that this can only be explained by supposing that additional isolating mechanisms have been at work.

Some Special Considerations

Hardy (1953) has pointed out that the Greek word plankton means 'that which is drifted' and it is generally assumed that plankton consists of small animals which are either unable to swim or only capable of swimming weakly, yet a large euphausian, *E. superba*, which has been observed *from a jetty* to stem and even swim against a current of one-third of a knot (E. R. Gunther, unpublished notes) is regarded as planktonic, and indeed its behavior in the open ocean is certainly the same as that of the smaller and less powerful swimmers of the plankton. There is perhaps an important factor involved here for in the open ocean there are no fixed points of reference by which animals can maintain a position independent of the water movements, and in fact there is no reason to suppose that the animals are in the least 'aware' of the movement of their environment. Thus quite large strong-swimming animals may be essentially planktonic, in the absence of any specific directional stimulus, until they reach a region of unfavorable conditions, when it can be assumed that they use some power of movement to regain a favorable environment. For the purpose of this paper, however, plankton is regarded as consisting of those animals which are not capable of sustained horizontal movement in one direction. This assumption means that horizontal separation of one population from another of the same species could be an effective isolating mechanism if the distance apart of the populations were sufficient to prevent mixing either by turbulence or by the random movements of the individuals in each population.

Such a simple explanation would of course only prove effective in populations which remain for a long time within a uniformly moving layer, and even in such a case large scale eddies might tend to cause mixing, not only of the water but of the animal populations as well; nevertheless it is not inconceivable that simple geographical distance within a single water mass could be and probably has been effective in the evolution of many of the species found at present. Dowdeswell and Ford (1953) and Sheppard (1953) have shown that significant genetic changes can be caused by natural selection in less than ten years. For many tropical planktonic species which have a number of generations in a year this time might be even shorter.

Although there is probably no evidence that planktonic species in the sea are divided into small separate populations, though 'patchiness' and uneven distribution have long been established facts, the work of Baldi (1946) has shown that, in the continuous and relatively homogeneous conditions of Lake Maggiore, spatially separate populations of copepods exist, which can be recognized by significant dif-

ferences in the measurements of a number of characters, and which are presumed to be genotypically distinct. In this particular case isolation by distance alone may be postulated as the cause of this rapid microevolution, and it is most interesting to see that in one case the distance between the populations studied was as little as one kilometer.

If the same sort of population structure as this occurs in the sea some revision of the present views on species distribution may well be necessary, for it means in effect that every pair of breeding animals is a potential swarm, population, and, ultimately in suitable conditions, species. But even if a number of species have arisen from this cause it is fairly certain that selection would operate against a species divided into small discrete isolated units because such populations cannot exploit the whole potential adaptability of the species, but can only exploit the gene reservoir of each small unit. This may be done rapidly, but with a changing environment, and for most planktonic species, very small changes may be disastrous to populations so closely adapted to their environment; such units will probably be unable to adapt themselves to the new conditions. There is some evidence which suggests that these animals are closely adapted to their environment; for instance there are very few oceanic species which can be kept alive in captivity for more than a few hours and although this may be a result of factors such as accumulation of waste products, or the damage caused by contact with aquarium walls it may equally well be caused by small changes in temperature, salinity, or pH. The use of planktonic animals as indicators of otherwise almost undetectable hydrological differences between water masses is evidence of great sensitiveness to minute environmental changes. The known distribution of oceanic species shows that there are only a few really cosmopolitan species and these are usually inhabitants of the deeper water layers where environmental conditions may be even more uniform than elsewhere in the oceans.

Environmental conditions must inevitably change, and one can assume that in the history of the oceans many small highly specialized species have become extinct, because in a small population the chances of an advantageous mutation, or recombination of genetical material arising, are so much less than in a large population. From this one can conclude that any mechanism which in the uniform conditions of the ocean facilitates the gene flow throughout the whole of a species and which is effective in preventing isolation of parts of a species will, in a changing environment, have been at a great selective advantage.

One such mechanism can be found in the habit of vertical migration, a habit which is widespread and which has been evolved independently by almost every animal group in the plankton.

A Possible Mechanism for Restricting Speciation

It is an almost invariable rule that the speed of movement of water in the oceans is greatest at the surface and progressively slower with increasing depth. Thus it follows that any animal which descends below the immediate surface layer, and very many plankton animals seem capable of vertical movement, is retarded in relation to movements at the surface. It may well be that the main selective advantage of at least diurnal migration is that if both phyto- and zooplankton are patchily distributed any patch of herbivorous zooplankton which was not in contact with a patch of phytoplankton would, by its inability to move horizontally, starve, yet by moving vertically down to a slower moving layer would alter its position relative to the patch of phytoplankton (limited by its light requirements to the surface layer), and on rising again would in all probability increase its chances of meeting its food. This view is taken by Hardy (1953), but it can be argued against it that it does not

take account of seasonal and breeding migrations, and also that not all planktonic animals are herbivores, though in the latter case, the carnivores would follow the movements of their herbivorous prey.

A 'navigational' advantage has also been postulated for vertical migration, and indeed in the case of seasonal migrations distributional studies seem to confirm this function (Mackintosh, 1937) but it is difficult to imagine how oceanic conditions could have remained so stable and so precise for so long that they could have allowed the exact current speeds and directions necessary for the evolution of such a mechanism.

The alternative suggestion put forward here is that the main function of vertical migration is to mix up populations and to facilitate gene flow throughout a species, thus preventing the effects of spatial isolation from causing a disastrous collection of small specialized species unable to adapt to changes in their environment.

For vertical migration to bring about mixing it must be a rather unprecise affair, for if one considers two animals or two patches of animals at some distance apart which migrate from one layer to another which moves at a different speed or in a different direction, it is at once apparent that if each spends the same amount of time in each layer then there is no more chance of their meeting than if they remained in one layer only. Certainly if one patch migrates at a slightly different time to the other, earlier or later, there may be a stage when its distance from the other patch is altered, but the original distance apart will again be resumed later in the cycle. If, however, in each patch some animals migrate sooner than others in the same patch or alternatively some go deeper than others, then a general dispersion of the groups will occur and the chances of their meeting other groups are greatly increased.

It has been shown by studies of vertical migration that populations tend to be dispersed over a more or less wide range of depth when they are not concentrated at the surface (or the bottom in shallow water), and that the ascent and descent is often a gradual process; indeed Cushing (1951) showed that some diaptomids and a *Daphnia* were able to climb at 3.5 m/min but that the normal speed of their migration was 4 cm/min.

In certain euphausiids the speed of migration may be high, but Baker (1959) has shown that in *E. triacantha*, a species which Hardy and Gunther (1935) indicate as making very rapid vertical movements, the population is spread over a wide range of depth both by day and night, and though a large part of the population moves towards the surface at night there is no marked concentration in the surface layer. A population structure of this kind must be very effective in preventing spatial isolation as it will ensure continuous horizontal dispersion, and indeed Baker has shown that there is no evidence at all for swarming or 'patchiness' in this species.

Even in those diurnally migrating species which form marked concentrations at the surface, the ascent and descent are not performed simultaneously by the whole population, but gradually over a period of time, giving the familiar picture, which in one form or another is illustrated in so many papers on the subject, in which the population structure in the late afternoon and early morning is represented by a long, almost parallel-sided column from the surface to the depths.

Russell (1927) mentioned [vertical] 'changes due to spawning habits' as one of the categories into which he classifies vertical migration, and quotes as examples of animals which perform this kind of migration certain medusae and salps. Since that time quite a number of other animals have been shown to perform vertical breeding migrations. Certain oceanic fish, whose larvae are planktonic (even though the adults may not be) (Bertelsen, 1951), quite a number of chaetognath species and some euphausiids are examples,

and it is likely that more will be found as more investigations are made.

It is difficult to see any selective advantage in such migrations, other than that of mixing, though David (1958) has suggested that in certain Chaetognatha the habit may be analogous to the return of terrestrial Amphibia to water at the breeding season, as a relict habit derived from some deep-living ancestor. Though it is possible that there is a 'navigational' advantage in this type of migration, this is certainly unlikely in the case of some of the Chaetognatha, for these descend to a depth of about a thousand meters to lay their eggs which then rise towards the surface, hatching at about 200 meters, apparently regardless of the speed, direction, or number of water layers through which they pass. While the mature adults may be less liable to predation in the comparative darkness of the deep water the highly vulnerable young stages are found near the surface, and it seems unlikely that the advantage of this migration lies in protection from predators. On the other hand, as a method of mixing it is bound to be a most efficient mechanism in cases where spawning is a more or less prolonged process as is the case for example with *Sagitta gazellae*, for in effect the breeding individuals release a stream of eggs and larvae over a period of time from an almost stationary spot into the moving surface layer, and the chances of the products of separated breeding animals meeting are thereby greatly increased in comparison with those which breed and spawn in a uniformly moving layer.

In the case of seasonal migration, which is such a common habit among animals in higher latitudes, it is not easy to see how it can be of much advantage in mixing populations. It normally takes place over a longish period, perhaps a month or so in the case of certain Antarctic species, and as the species do not appear to migrate simultaneously throughout their range, it could have some effect in mixing the population, but despite the objections to the evolution of this habit mentioned earlier more probably the advantage of this migration is navigational as Mackintosh (1937) has suggested.

Some Supporting Evidence

The hypothesis put forward here to explain what Hardy (1953) has described as "the meaning of such migration in terms of advantage to the animal," is regrettably speculative and what evidence there is which might support it is both slight and circumstantial; nevertheless the hypothesis does offer an explanation for one or two otherwise unexplained facts. It is a generally accepted fact that the number of planktonic species in the oceans increases from the poles to the equatorial regions, although exact figures have been worked out only for very few groups, e.g., euphausians (Zimmer, 1956; Sheard, 1953). This paucity of species in the high latitudes is difficult to explain, unless spatial isolation of small populations has been to some extent responsible for the evolution of new species, for then it would be expected that in areas of relative calm and slow water movements the effects of mixing of populations by vertical migration would be less effective than in the high latitudes where total winds are considerably greater. It is perhaps of importance to realize that this difference in wind speed from the equator to the poles will have been always present regardless of the shape of the ocean, being essentially dependent upon the shape and rotation of the earth. In support of this view is the fact that many of the Southern Ocean species have an even and fairly continuous distribution. All that have so far been studied or are being studied at present, with the notable exception of *E. superba*, have such a distribution, and the work of Baker (1954) on circumpolar continuity suggests that such continuous distribution is the rule rather than the exception. In tropical waters, however, species seem much less uniformly spread. Wilson (1942) gives analyses of the plankton

copepods, station by station, which suggest that the discontinuities are more than simple, small scale, 'patchy' distribution. It is possible, however, that the discontinuities are due in part to our very inadequate knowledge of the tropical regions, for the recent work of Brinton (in press), Bieri (1959), and Sund and Renner (1959) based on extensive series of cruises by U.S. ships in the Pacific have gone a long way to explaining the complex pattern of distribution in that ocean.

Euphausia superba has been mentioned already as an exception to the normally even distribution of animals in the Southern Ocean and its curious distribution is possibly explicable on the basis of the hypothesis put forward here. It is a strong swimming form which spends its life in closely packed shoals (J. W. S. Marr, personal communication). It may perform a breeding migration; certainly the eggs hatch in deep water which from a mixing point of view is the same, but it does not perform a seasonal migration and apparently little if any diurnal migration, yet in some way it retains the identity of each shoal from the larval stage to the adult, a type of distribution which would be expected to restrict the adaptability of the species, and indeed its distribution is curiously asymmetrical (Marr, 1956), since it is confined to the regions of the East Wind and Weddell drifts while the remainder of the West Wind drift area though hydrologically almost indistinguishable from the Weddell drift is very sparsely populated.

Conclusion

If the hypothesis that mixing by vertical migration inhibits the formation of too many species with too little capacity to survive changes in the environment is accepted, then one may assume that in the tropical areas where this mixing would be less effective there may be species which have evolved in the same water mass which may be closely adapted to the same conditions; if these should come together the so-called Gaussian hypothesis suggests that they will be unable to coexist. However, Fryer (1959) has shown that when there is a high degree of unspecialized predation there can be coexistence of very similar species dependent on the same food supply and it is possible that an analogous situation may exist in the oceans. Alternatively, quite small differences in the feeding mechanisms of closely related species may ensure that they do not compete for their food supply, and small differences in depth distribution or behavior would have similar effects. While many factors have been shown to control vertical migration in various groups and species (Cushing, 1951) it is suggested that the selective advantage of this migration may be the same for all marine forms.

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Certain Comments on the Subspecies Problem

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SINCE Wilson and Brown (1953) in their paper, *The subspecies concept,* first opened the discussion on this matter, numerous papers and symposia have centered around the question of the tenability of the subspecies and of trinomial nomenclature in general. The problem has remained largely unsettled in spite of the numerous points of view that have been expressed. The great interest that has been shown, and the diversity of opinion, surely indicate that a real problem exists. The lack of general agreement also may indicate a lack of communication between the holders of the divergent opinions. Serious workers do not expend this much effort in discussing concepts in areas of knowledge where unanimity of thought is reached upon the general dissemination of the facts.

What then are the differences that lead to such a lack of agreement? It is not the purpose of this paper to review in detail the course of these discussions, but rather to examine if possible, some of the reasons for the divergence of opinion.

The papers that have appeared pro and con on the subspecies problem tend to fall into two main and basically opposing groups. One group (Brown and Wilson, 1954, and Gillham, 1956, as examples) would dispense with the subspecies entirely, as of little or no value. Others (as Fox, 1955, and Durrant, 1955) defend the subspecies concept as valuable and useful. In between these opposing points of view, we find those who would redefine the subspecies and limit its application, without discarding it. Among these may be included Edwards (1954), Pimentel (1959), and van Son (1955).

Since the connotations of the subspecies concept extend in fact far beyond the terse and limited definition that appears in the Rules, it seems that one basic difference of opinion stems from a possibility that the term, subspecies, means distinctly different things to different workers. Here, then, the disagreement is centered in semantics. In the course of the many discussions the writer has heard on this matter, he has had the feeling that the opposing individuals have not always been talking about the same thing. Edwards (1954) and van Son (1955) have proposed some definition of the term subspecies that would bring the meaning of the term to one objective and common concept.

These various levels of meaning for the term, subspecies, may be more deep-rooted than at first appears, and it is possible that a generally stated definition of the term will not in itself settle the matter. Part of the difficulty arises from the differences in the organisms that are studied by the various workers. It seems apparent that defenders of the subspecies are more numerous among entomologists who work with the more plastic groups of insects. In these groups the great variation among what appear to be closely related species groups makes it desirable to have some generally accepted taxon by which to express this variation.

Workers in some other groups, where variation either is not so great, or in which study has so far not revealed the presence of such variation, are less insistent that the subspecies is a necessary unit in classification.

Workers in vertebrates present a third situation, and from among their ranks have come some of the most serious objections to the use of the subspecies concept. If we recall that in total numbers of species vertebrates are rather few,

and that at least certain groups of vertebrates are fairly homogeneous in structure, it is evident that the great popularity of the vertebrates and the large number of workers they have attracted have resulted in a frequent reworking of at least some of the more popular groups, such as birds and small mammals. This has led to a refinement of methods and procedures to a point where it is necessary to have a large series of specimens and to devote considerable effort to determine whether a given population belongs to one or another described subspecies. Here the distinctions between subspecies are of relatively small scope and workers in groups outside the vertebrates can scarcely be qualified to pass judgment.

By contrast, insects are the most numerous, both in number of species and individuals, of terrestrial Metazoa. Admittedly insects are less studied, and less well understood, than are some other groups. This is inevitable, if one takes the number of organisms to be considered, and divides this by the number of workers available to undertake such study. Only a very few popular groups of insects, such as butterflies and mosquitoes, have received attention approaching that given to certain vertebrate groups.

This suggests that the subspecies as conceived by many entomologists is a more inclusive thing than it has become in dealing with certain of the vertebrate groups. The entomologist who defends the subspecies concept is not really defending the same level of classification that exists in the treatment of certain vertebrate groups.

It may be pointed out in clarification, that certain insect names, now considered at the level of subspecies, were held for years at the level of species before being reduced to subspecific status. Among the butterflies, many of these names apply to organisms differing markedly in size, coloration, behavior, and food plants, but which are considered to be subspecies on the basis of structure, distribution, and the common sharing of characteristics that appear to outweigh the easily visible differences. As an example, the nymphalid *Euphydryas editha* in some subspecies feeds as a larva on *Plantago;* in other subspecies the larval food is *Pentstemon.* The alpine subspecies *nubigena* has scarcely half the alar expanse of the nominate *editha.* In the nymphalid genus *Speyeria,* the western subspecies of *cybele* have bright reddish males and very dark or blackish females. The subspecies of the eastern United States are fulvous in both sexes.

It is not suggested that all subspecies among vertebrates are of small scope, nor that no subspecies of small scope have been proposed among the insects, but rather that in at least certain groups of insects, the plasticity of the organisms makes the subspecies concept extremely useful, and to abandon its use might well result in problems that would present considerable difficulty.

Another and totally different cause of disagreement would seem to center around the possibility that we are attempting to use our system of classification for two distinct purposes, which may not always be mutually in accord. Originally (and this is to a great extent still true) the naming of organisms was undertaken to bring order out of chaos. Man's mind is so organized that he finds it easier to deal with groupings of small extent rather than with large heterogeneous assemblages. So he breaks unwieldy masses down into units of a size that can be treated more effectively and then sets these smaller units into relationships one with the other. It has been noted by semanticists that man's mind tends to work in dichotomies. Whether such a method of approach actually reflects conditions as they exist in nature can scarcely concern us. Man has no other tool than his mind with which to deal with nature, and his efforts along these lines must be within the limits of the tool he possesses.

Systematics is thus an attempt to sort information into a usable form. Organisms without names are without meaning to science. The fact that such organisms

must exist is beside the point. Without naming, and thus bringing the organism into our system, such an organism remains unrecognized. Workers are accustomed to say, for example, that a given genus includes a certain number of species, as though the names on the list were the species and the possibilities had been exhausted. The names on the list are man's way of recognizing the existence of certain entities he calls species, and while the list may in fact represent all the permutations of a given set of characters that the worker is willing to recognize, quite as often the list may more accurately depict merely the incompleteness of man's knowledge of this group.

Along with this practical listing of names for convenience has developed the attempt to express by systematics the relationships of one organism to another. Phylogeny has been superimposed on naming and the same system has been used for both, with more or less success. The success must depend on the skill of the worker and also in part upon the extent of knowledge that has been gained about a given group of organisms. However, it seems worth mentioning that phylogeny was not the original goal of taxonomy, but was added after the system was already set up. Phylogeny is in some respects a different science from the taxonomy of organisms. Attempts to express relationships through our system of naming are very useful and it is not suggested that such attempts should be discontinued. In fact, phylogeny makes systematics live, to an extent that naming alone could not do. But some thought might be given to the original reasons for setting up our present system, and that phylogeny was not the original goal. It may well be that the ultimate concepts of phylogeny could be expressed better by some other method than our current system of nomenclature. Nor should phylogeny be allowed to obscure the original goal of taxonomy: that of giving names to unrecognized organisms. Not all names can wait until phylogeny is well understood in all groups.

In connection with man's systems, of which zoological nomenclature is one, we are faced with a concept that has been expressed more frequently by semanticists than by zoologists. Man cannot deal with a multiplicity of diverse objects or concepts without some system. To facilitate his treatment of things in the universe, he devises systems, of which nomenclature is one. Since his only contact with the material is through the systems he devises, he sooner or later comes to believe that these systems actually reflect the conditions that exist in nature. This may or may not be so. It is possible that our system is an accurate analysis of relationships as they exist in nature. It is equally possible that such is not the case. We should, I feel, have a mental reservation that our systems exist more in our mind than in nature. However useful our system may be as a tool, we cannot assume that no other system could be devised to express the same concepts as well or even better. By this line of reasoning, the concept of subspecies should no more be under fire than any other level of classification, since all are equally the products of man's ingenuity.

It has been stated many times that there is no objective proof in science. If a system or theory does not work, then this is philosophically valid. However, should the system or theory appear to work or to explain the problem under analysis, the validity is not established, since the universe has not been exhausted and we cannot demonstrate that there exists no other system or theory that would serve as well. Most problems (like many equations) have several solutions or roots from which we select the solution that best fits the situation at hand. Our present system of classification is such a choice. It has needed modification over the years to allow for the inclusion of concepts of phylogeny, genetics, and zoogeography that were not current when the system was first proposed, and it is

little wonder that these changes have caused some discussion. It is even more remarkable that the system has worked as well as it has, considering the advances that have been made since it was first proposed. However, to single out the subspecies concept for attack seems unjustified. This concept is only one of several that have been incorporated into the system to allow greater flexibility.

While most recent workers accept the existence of levels of population below the species, there is disagreement on how such populations should be treated. One of the points frequently made is that subspecific names are not given to biological entities. Whether or not a name proposed as subspecific actually applies to a biological entity is not easy to decide. Any answer is certain to be colored by individual points of view as to what such an entity may be. Without doubt, some proposed subspecies will prove not to be entities by any biological standards. But certainly others will withstand the usual criteria. We find ourselves faced with a dilemma: must we withhold names until we are certain what a biological entity really is? If this be the case, many unrecognized segregates must remain unnamed indefinitely. I doubt that any generally accepted definition of a biological entity will be found in the immediate future. It may be that the workers who object to subspecies on these grounds are saying that the subspecific segregates do not meet their own standards of a biological entity. Is it too much to propose that complete understanding of the biological distinctness of a population is not a necessary prerequisite to recognition by a name? It might be argued that the value of having a name for an otherwise confusing population outweighs the shortcomings of our system.

Among the objections that have been raised to the naming of subspecies that concerning discordant variation versus concordant variation has received considerable recent comment. Gillham (1956), and Wilson and Brown (1953) in particular have presented views on this matter, and Edwards (1955) has presented evidence against the occurrence of concordant variation as a norm. His arguments were based on genetics. A word might be appended on the role of the environment as a selective screen in this process. Characters are presented by the organism to the environment, as units or linkage groups. The organism thus presents to the environment a group of unit or group characters, and the environment selects each unit or group independently of the others. It must follow that the selection of a single character or a linkage group is a separate process from the selection of other single or linked characters. It would seem that complete concordance in the selection of all of an organism's characters would happen rarely and only by chance. Discordant variation would be much more likely to be the norm. If such an explanation be true, then the insistence upon concordance of variation as a prerequisite of recognition for a population would seem untenable.

Nothing in this discussion is intended to support the trinomial for use in naming variants of less than population level. Individual variants, seasonal forms, and similar variations occurring within a population pertain to a level of infraspecific treatment that is without recognition at the level of priority. Such study is of great interest to the student of variation, but is outside the field of systematics. However, if no population below the level of species is to be recognized by priority, some of the flexibility and usefulness of the system is lost. The general use of the concept of subspecies in the classification of many groups should attest that populations less than species are more easily grasped in relation to species populations if left within the usual framework of systematics. It is natural that errors of judgment have occurred and will occur again, and that names have been given where they should not have been given. But it is doubtful that the number of errors is greater than that to be found in

other fields of endeavor. No system is to be judged entirely by its mistakes, but rather by successes. When it is found that subspecific names do not really represent populations, it is as much the function of the taxonomist to synonymize these as it is to recognize those that deserve recognition.

In practice, the use of the subspecific concept has in many cases resulted in improvement in the classification of a group. In birds, the total recognized number of full species has dropped from about twenty-five thousand to less than five thousand, due largely to consolidation brought on by application of the subspecies concept. Certainly this represents more accurately the conditions as they exist. In the butterfly genus *Speyeria,* the reduction in the number of recognized full species has been similar. Dyar, in 1902, recognized 37 full species and 15 subspecies. Dos Passos and Grey, in 1945, recognized 13 species and 95 subspecies. The increase in total names is due mostly to descriptions dating since the time of Dyar's List, and may be excessive. Yet few can be found who will argue that the arrangement of Dyar is preferable. In these instances the use of the subspecies concept has allowed for a consolidation of knowlege and a more realistic view of relationships than might exist without its use.

It has been stated, and with considerable evidence, that many subspecific names have been given to populations that in degree of variation represent points along a cline. Most workers agree that the naming of more or less arbitrary points along a "smooth" cline is inadvisable. Many workers seem to feel, however, that the naming of populations at the "steps" of a "stepped" cline is acceptable, or at least less undesirable.

It would appear that the cline has been asked recently to subsume more than it was originally intended to do. Examples of truly "smooth" clines are probably not as numerous as some would think. Conversely, it may well be that the so-called "stepped" cline is not always a cline at all in the true sense of the word. It may be merely a graph of points at which variation breaks, and may be more of an artifact caused by the presentation of the material than an actually existing condition in nature.

For practical as well as theoretical reasons, there must conceivably be a limit to the number of names that can be applied to one series of variations. And the least satisfactory condition for applying names is along a "smooth" cline. However, there lingers the suspicion that the invoking of clinal variation has at times served as a way of avoiding a problem that might have been more difficult to solve in another way. Not all variation can be dismissed merely by saying that it may be clinal. It is difficult to see how such a large portion of variable species can follow clinal variation as has been claimed. Where recognizable variation exists to apply no generally acceptable names is not a solution. No problem was ever solved by avoiding it.

As an example, the dark-colored populations of the nymphalid *Euphydryas chalcedona* may be treated as clinal, but the picture is probably better reflected when considered as several centers of variation separated by blend zones.

It has been pointed out, and with telling effect, that many subspecies have been recognized on the basis of two few characteristics, or upon poorly chosen characteristics. Certainly such actions have occurred. However, the blanket statement made by critics, that slight color marking forms the only differences between subspecies, is not always a valid criticism. Diagnostic markings and other often slight external characters must of necessity form the prime criteria for discriminating specimens in the cabinet. Other and more important differences are lost upon the collection of the specimen and cannot be studied except in the living organism. Any population that is sufficiently distinct to attract the interest of a serious worker has certain attributes that

are tacitly acknowledged. Among such attributes we may consider: (1) such a population occupies a range, (2) it sustains itself out of its own genetic resources, (3) it has some degree of isolation from other similar populations, (4) it has a somewhat different gene pool from related populations, due to the cutting off or lessening of gene flow between it and the adjacent populations. These are the true important differences. The differences in appearance are the convenient marks for recognition of specimens.

With the differences mentioned above often go differences in behavior, phenology, and food plants. As an example of highly differentiated subspecies, that are not always easily separated by color alone, may be cited those of the lycaenid butterfly, *Philotes battoides*. Of these subspecies we may consider three. The nominate *battoides* is a high altitude, cold-adapted population, feeding as larvae on small "rock garden" species of *Eriogonum*, and emerging very early in the year for the elevation at which it lives. The subspecies of southern California, *bernardino*, is small to tiny in size, living in a relatively warm region, emerging in late spring or early summer, and feeding as larvae on the shrub, *Eriogonum fasciculatum*. The subspecies *martini* is found in the desert region along the Colorado River in Mohave County, Arizona, emerging very early in the year, and feeding on a still different species of *Eriogonum*. It is true that each of these subspecies has diagnostic markings recognizable to the initiated, but these seem trifling compared to the factors other than markings which separate these populations. If the concept of subspecies were to be dropped, a distinct regression in the systematics of this genus would occur. Personally, if faced with the none too attractive alternative of not recognizing these populations at all, or of elevating them to specific level, the latter choice would seem preferable. The concept of subspecies appears so made to order for such a situation that it seems entirely unnecessary to propose any alternative treatment.

Differences of a magnitude of those mentioned above must reflect profound physiological differences as well. Insect physiology is not practiced by enough workers for physiological differences between populations to be demonstrated in every instance, prior to description. However, it would be most valuable if this could be done for at least some populations, as a means of verifying a condition that reasonably must exist.

In summing up, it is suggested that some of the sources of disagreement as to the value of the subspecies concept may be found in the way in which man thinks, in the attempt to use our classificational system for two not always congruous purposes, and in the differences inherent in the groups of organisms studied by various workers.

In defense of the use of the subspecies concept, it may be mentioned that in our present system of classification the subspecies is the category expressly provided for the treatment of populations less than species. That this tool is imperfect must be admitted. But to admit imperfection is not necessarily to reject the tool entirely. The point of view is held here, that the good results outweigh the objections that have been brought forward.

As a final word it may be in keeping to remind ourselves that while excesses have occurred in the use of the subspecies, excesses have also occurred at other classificational levels. And while certainly not all subspecies are equivalents, neither are the described units at other categorical levels. And while our system may be in need of some alterations, the better to fit it for the job it must perform, these alterations may well be considered at all levels of category, rather than to single out the subspecies alone for criticism.

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The Structure of the Genital System of Pogonophora[1]

A. V. IVANOV

EVERYTHING known to date concerning the organization of the Pogonophora bespeaks the presence in them of sexual multiplication only. Caullery's (1944) considerations concerning external budding in *Siboglinum weberi* Caullery have not been confirmed, nor has the idea recently expressed by Jägersten (1956) of the existence of internal budding. The internal bud—the "endobody" described in *Siboglinum ekmani* Jägersten—is probably an artifact, the result of invagination of a portion of the trunk inside the adjacent part of the body.

Pogonophores are bisexual and lack sexual dimorphism; the sexes differ only in the position of the paired gonopores. In males the gonopores are rounded or slitlike and are located at the mesosome-metasome boundary ventrally (Fig. 1, *gp*). In females the gonopores are located laterally in the central part of the metasome somewhat anterior to the area of constriction of the anchor papillae (Fig. 9, *gp*).

The highly characteristic features of the genital system of Pogonophora are: the presence of a single pair of gonads lying in the trunk; the localization of the gonads in males in the posterior half of the metasome and in the anterior half in females; and the transformation of the pair of metasomal coelomoducts into genital ducts (Ivanov, 1955a).

Male Genital System

The male genital system of pogonophores has not been studied to date. The paired gonads found by Jägersten (1956) in *Siboglinum ekmani* in the anterior part of the metasome which he was inclined to regard as testes are actually ovaries. The first investigator of the pogonophores (Caullery, 1944) observed spermatic ducts in a section through the trunk of a male *Siboglinum weberi* and spermatophores enclosed in them; he represented them on his figures but was unable to guess their nature.

I have studied the male genital organs in *Polybrachia annulata* Ivanov, *Lamel-*

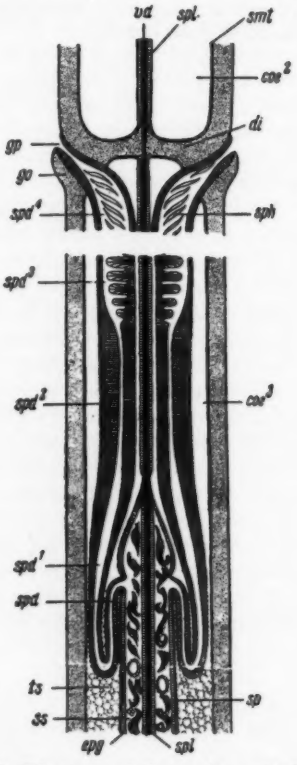

FIG. 1. Diagram of the male genital system of *Lamellisabella*.

[1] Translation of this paper has been furnished by the National Institutes of Health, Public Health Service, as part of its Russian Scientific Translation Program. The original article appeared in Zool. Zhurnal, 1958, vol. 37:1363–1374.

lisabella zachsi Uschakov, and partly in *Siboglinum caulleryi* Ivanov, by means of transverse sections stained with borax carmine, iron hematoxylin, and Mallory's method. The male genital system consists of a pair of sperm sacs and a pair of tubular spermatic ducts.

Sperm Sacs. In *Polybrachia* and *Lamellisabella* the sperm sacs extend from the level of thickening of the anchor papillae (Ivanov, 1957) to the posterior end of the body, that is, they are developed throughout the posterior section of the preannular and the entire postannular area of the metasome. They are quite broad channels (Fig. 1, *ss*) which abut laterally directly on the dorsal portion of the mesentery, which, together with the dorsal vessel, forms a vertical septum between them.

The sperm sacs are separated from the ventral longitudinal vessel by a considerable space, but anteriorly they are so broad that they fill the entire space between the dorsal and ventral body walls (Fig. 2, *ss*). The wall of the sacs consists of ciliated epithelium (Fig. 2, *eps*) which represents a continuation of the splanchnopleure that covers the mesentery and the dorsal longitudinal vessel (Fig. 1, *spl*). Correspondingly the basement membrane of the wall of the sacs is continuous with the terminal lamina of the mesentery and the intima of the blood vessel. In the vertical septum between the sacs all the characteristic elements—peritoneal cells, including groups of tall excretory (chlorogogue) cells (Fig. 2, *spl*), and the plasma myocyte bodies of the dorsal vessel —encountered in other parts of the body are maintained. Externally, the sperm sacs are covered with a very thin layer of circular muscle fibers and peritoneal epithelium.

The ciliated epithelium, however, is well developed only in the anterior parts of the sperm sacs, where it consists of

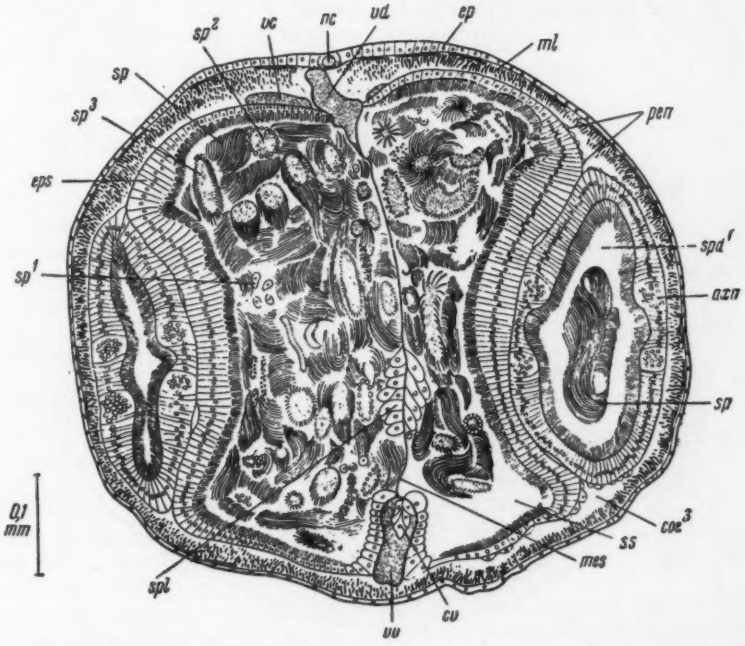

FIG. 2. Transverse section of a male *Lamellisabella zachsi* at the level of the anterior parts of the sperm sacs.

ciliated cells (Fig. 2, *eps*). Somewhat posteriorly, only a narrow longitudinal ciliated strip located on the ventrolateral wall remains in each sac (Fig. 3, *b*, *c*); elsewhere the epithelium has lost its cilia and takes the form of a quite loose layer of large clear cells (Fig. 3, *eps*). Finally, in the postannular sections of the sacs this layer is hardly developed and not uncommonly only the ciliated strips are preserved. They consist of large, well differentiated cells with long cilia (Fig. 4, *bc*).

In the cavity of the sperm sacs there is fluid containing a mass of floating male genital cells. These cells are in the most varied stages of spermatogenesis, beginning with spermatogonia and ending with mature sperm; they form characteristic packets consisting of cells of a single stage (Fig. 5). Among them there are sometimes solitary, comparatively large, rounded cells that constitute the spermatogonia. A following stage is represented by groups of four connected cells (Fig. 5, *a*). With their further multiplication characteristic multicellular complexes are formed which, by analogy with similar structures in oligochaetes, may be called "spermatospheres" (Fig. 5, *b*). Part of the cytoplasm of the cells is centrally confluent, forming a single common anuclear cytoplasmic mass, which merits the name of "cytophore" (Fig. 5, *cph*); the cells are arranged around the surface of the cytophore with which their cytoplasm is connected. The spermatid stages also remain attached in the spermatosphere (Fig. 5, *c*). Some time after their formation the sperm are liberated from the cytophore. The mature sperm are filamentous and consist of a thin, markedly elongated head and a very long tail. Sometimes, the early stages of spermatogenesis are clearly predominant in the anterior sections of the sperm sacs, but usually all the stages are mixed together and are encountered everywhere (Fig. 2, *sp*. sp^1, sp^2, sp^3). The question whether compact groups of gonocytes that might be regarded as testes exist anywhere on the walls of the sacs remains unknown. There-

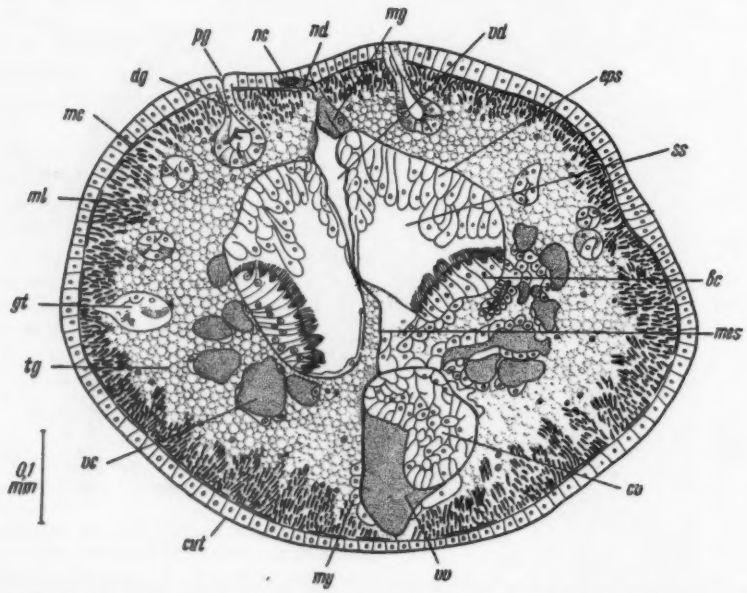

FIG. 3. Transverse section of a male *Lamellisabella zachsi* somewhat anterior to the annuli.

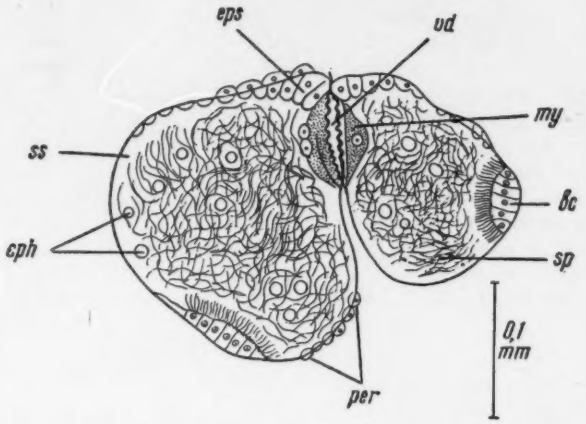

FIG. 4. Transverse section of the sperm sacs of *L. zachsi* in the postannular area of the metasome.

fore, the sperm sacs clearly deserve this name. In general they resemble the sperm sacs of oligochaetes and leeches and, as in these annelids, represent specialized parts of the coelom and their walls are modified coelomic epithelium.

The general appearance of the fluid from these cavities containing spermatospheres also resembles the content of the sperm sacs of oligochaetes and leeches. Incidentally the union of maturing male genital cells into characteristic groups, such as the spermatospheres, and the floating of genital cells in the coelomic fluid, as seen in other invertebrates, i.e., bryozoans and phoronids, is not like what is found in annelids.

The strips of ciliated epithelium on the walls of the sperm sacs probably serve for the movement of the fluid containing the genital cells, and the beating of the ciliated epithelium in the anterior parts of the sacs apparently pushes the groups of sperm cells into the genital ducts. The presence of the dorsal blood vessel in the septum between the sperm sacs assures an adequate influx of nutrient substances to the developing genital cells. As I have shown previously (Ivanov, 1955), the dorsal blood vessel contains arterial blood enriched with nutrient material.

Spermatic Ducts. The anterior ends of the sperm sacs communicate with the spermatic ducts (Fig. 1, *spd*^{1}-*spd*^{4}), which first loop backward and then extend forward along the sides from the mesentery to the mesosome-metasome boundary, where they open into the external gonopores ventrally located (Fig. 1, *gp*).

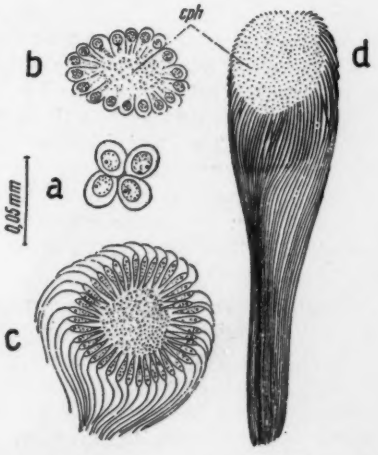

FIG. 5. Some stages of spermatogenesis of *L. zachsi*. *a*, stage of four gonocytes; *b*, group of spermatocytes; *c*, group of spermatids; *d*, group of sperm.

The spermatic ducts are thick-walled tubes covered on the outside with a thin layer of muscular fibers and peritoneum; they are attached to the abdominal wall by special thin mesenteries (Fig. 8, *mes*). The histological structure of the spermatic ducts, which changes considerably at different levels, was studied in *Lamellisabella zachsi*. Near the connection with the sperm sacs, the epithelium of the spermatic ducts (Fig. 1, *spd*) consists of tall ciliated cells, distinguished by interesting details in the structure of the root apparatus of the cilia. The root filaments, coming from the basal granules and forming, as usual, a characteristic cone, collect into quite a thick bundle, which extends to the basal end of the cell where it breaks up into separate filaments which become a confusing network of very fine fibrils. This creates the impression of a continuous basal reticular layer in the epithelium that connects the root filaments of the individual cells (Fig. 6).

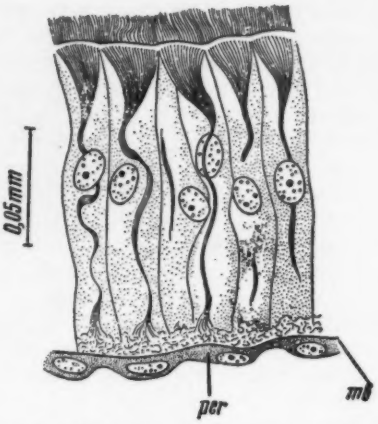

FIG. 6. Epithelium of a spermatic duct of *L. zachsi* near its exit from the sperm sac.

More anteriorly (Fig. 1, *spd*^{1}), the ciliated epithelium, directed inward from the wall of the spermatic duct, forms a deep longitudinal fissure. Large gland cells open into the bottom of the fissure. On the wall opposite the fissure there is a short longitudinal crest. Somewhat anteriorly the fissure widens to form a sulcus, bounded by convex tori, and similar tori are found on the opposite wall of the spermatic duct. The tori have a very distinctive structure; inside them there is a quite dense band of small cells without clear boundaries; in transverse sections this band looks like a compact accumulation of nuclei (Fig. 2, *axn*).

The central sections of the spermatic ducts are distinguished by the very thick walls, and, correspondingly, narrow slit-like lumen (Fig. 1, *spd*^{2}). The ciliated epithelial lining is preserved here, but the cells are overfilled with secretion.

Still further anteriorly (Fig. 1, *spd*^{3}), the lateral wall of the duct thins and loses its cilia, whereas the median walls thicken and form glandular crypts, within which there are bundles of cilia (Fig. 7, *cr*).

Finally, the long distal sections of the spermatic ducts which lie in the metameric region of the trunk (Fig. 1, *spd*^{4}) are formed of moderately tall ciliated cells (Fig. 8, *spd*^{4}).

The spermatophores are formed in the posterior parts of the spermatic ducts. Their walls are undoubtedly made of the secretion of the epithelial gland cells. The completed spermatophores lie in the distal parts of the spermatic ducts, arranged in a single row, parallel to each other; thereby they all have one end directed forward and outward, the other end, backward and inward (Fig. 1, *sph*). Each spermatophore bears a looped filament (Fig. 8, *fil*).

Since the spermatic ducts consist of ciliated canals by means of which sections of the coelom (sperm sacs) communicate with the external medium, they should be considered true metasomic coelomoducts.

Spermatophores. The spermatophores consist of thin-walled membranous sacs filled with sperm. I have described these structures, exceptionally characteristic of the Pogonophora, in many species (Ivanov, 1952, 1957). In the order Athe-

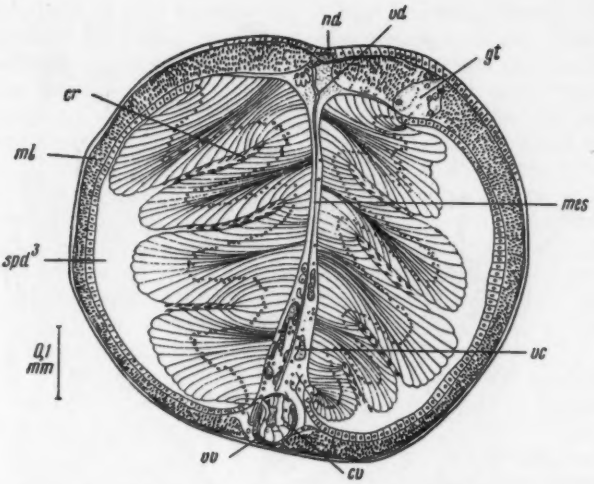

FIG. 7. Transverse section of male *L. zachsi* posterior to the metameric part of the metasome.

canephria they are spindle-shaped, in the Thecanephria, foliate. Their dimensions depend on the size of the animal. Thus in the very small *Siboglinum minutum* Ivanov, the spermatophores do not exceed 0.12 mm. in length, whereas in the large *Spirobrachia grandis* Ivanov they reach a length of 2.5 mm. The shape and size of the spermatophores are species characteristics.

At one end the spermatophore membrane extends out as an exceptionally long and fine thread that forms numerous loops applied to the spermatophore surface. When the spermatophore enters the water this filament probably straightens out and facilitates the floating of the spermatophore. It is possible that it hooks the spermatophore to the female tube.

The transparent substance of the wall of the spermatophore of *Lamellisabella zachsi* gives a positive reaction for polysaccharides when treated with the periodic acid-Schiff reagent.

Female Genital System

In the literature there are only sketchy and inexact data concerning the female system of Pogonophora (Caullery, 1944; Jägersten, 1956); the ovaries of *Lamellisabella* were described by Johansson (1939). I have investigated this system in the majority of the known genera. A study of sections of *Polybrachia annulata* and *Lamellisabella zachsi* has given a particularly complete picture. Sections were stained with Heidenhain's iron hematoxylin and Mallory's azocarmine.

In females a pair of very long ovaries is situated in the coelom of the anterior half of the metasome. Their anterior ends attach to the dorsal blood vessel behind the muscular diaphragm, and the posterior ends reach the level of the area of thickening of the anchor papillae. The oviducts, not connected with the ovaries, begin at this level; they open by gonopores somewhat anteriorly (Fig. 9).

Ovaries. In immature females the gonocytes appear directly behind the diaphragm on the lateral surfaces of the dorsal vessel beneath the peritoneum (Fig. 10, *gon*). The rudimentary gonads then proliferate markedly, penetrating into the coelom to a progressively greater extent along the sides from the mesentery

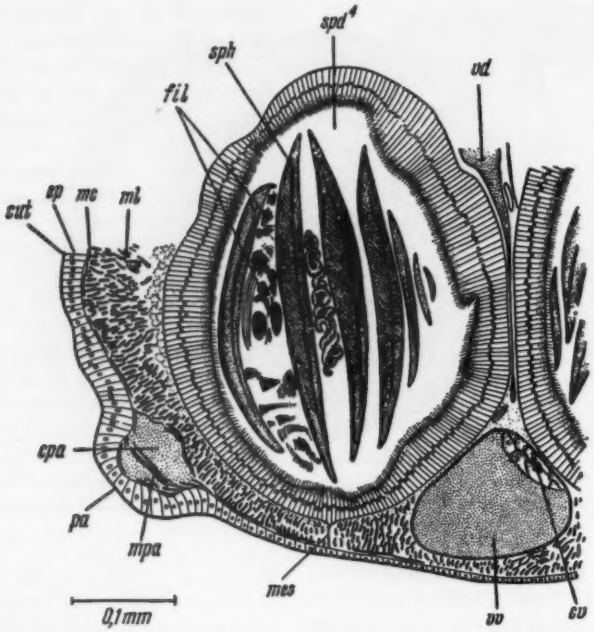

FIG. 8. Spermatic duct of *L. zachsi* and adjacent part of the body wall; part of transverse section of a male through the anterior part of the metasome.

and finally are converted into long sausage-shaped outgrowths that extend far posteriorly (Fig. 9, *ov*). Simultaneously the multiplication of peritoneal cells, from which the ovarian walls are formed (Fig. 9, *epo*), occurs on their surfaces. Longitudinal vascular branches which supply the growing peritoneal cells with nutrient substances and oxygen grow out from the dorsal blood vessel into the area of attachment of the ovaries (Fig. 11, *vov*).

The peritoneum of the ovaries consists of small, for the most part flat cells (Fig. 11, *epo*). Beneath the peritoneum is a thin limiting membrane connected directly with the intima of the ovarian vessels. The inner surface of this membrane lacks cellular elements but the vessels (Fig. 11, *vov*) are surrounded from all sides by tall cells sometimes arranged in several layers.

The number of vessels in each ovary varies from two to five in different forms depending on their size. In *S. caulleryi* and *O. dogieli* one vessel extends along the dorsal aspect of the ovary, another along its ventral aspect. In *P. annulata* and *L. zachsi* a third, ventrolateral vessel is added (Fig. 11). Finally, in *S. grandis* there are in addition vessels on the lateral and medial walls, i.e., every ovary is supplied by five vessels.

The ovarian cavities are usually solidly filled with genital cells and the large ovocytes can lie more or less loosely arranged only in their posterior sections (Fig. 11, *ov*). The anterior parts of the gonads where small oogonia are located are particularly compact. Posteriorly the size of the genital cells increases and their cytoplasm is progressively enriched with yolk granules and fat droplets. The largest oocytes and the mature ova occupy the posterior parts of the gonads (Fig. 9, *o*). A characteristic feature of Pogonophora is the absence of any follicular cells.

The posterior ends of the ovaries lie inside the cavities of the broad infundibula of the oviducts or even penetrate into the oviducts themselves (in many females of *P. annulata*). Here their membranes rupture and mature ova are poured into the lumina of the oviducts (Fig. 9).

Oviducts. There is no direct connection between the ovaries and the efferent passages. The latter consist of a pair of tubes bent into a U-shape. The medial wider limb of the tube may be called infundibulum (Fig 9, *inf*); the outer narrower limb may be called efferent duct or oviduct (Fig. 9, *ovd*). The infundibula abut on the mesentery on two sides and this then forms their common medial wall

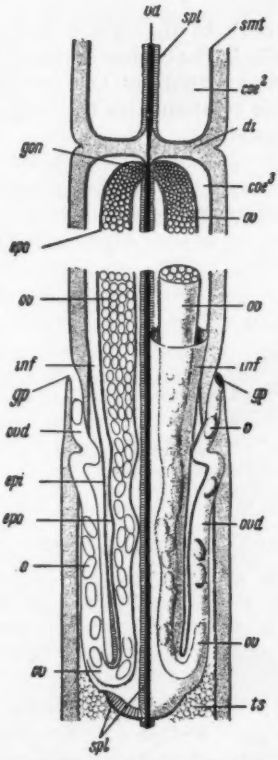

FIG. 9. Diagram of female genital system of a pogonophore; on the right side the infundibulum and canal of the oviduct are represented whole.

(Fig. 12, *mes*), hence the dorsal vessel lies between them. The anterior edges of the infundibula are attached to the adjacent body wall. The oviduct arises from the posterior end of the infundibulum. It is first directed forward between the body wall and the infundibulum; then for a short distance it passes into the longitudinal musculature of the cutaneous-muscular sac (Fig. 12, *ovd*) and finally opens to the exterior by a ventrolateral gonopore (Fig. 12, *gp*). All these relationships are best seen in the diagrammatic Figure 9.

The wall of the infundibulum consists of a low epithelium without cilia (Fig. 12, *epi*) which, incidentally, is considerably thickened posteriorly, particularly in the vicinity of the beginning of the oviduct, and is distinguished by its glandular nature. The epithelium has a thin basement membrane external to which occur scattered muscle fibers. Because the two infundibula occupy the entire space of the coelom, their outer surfaces, applied to the body wall, lack a peritoneal epithelium but this is present wherever the infundibula are in contact with the coelom. On the mesentery the characteristic cellular elements are preserved in the area of the infundibula, and specifically the rows of tall excretory cells are particularly well developed here as are the folds of splanchnopleure (Fig. 12, *spl*), supporting small lateral blood vessels.

The walls of the oviducts are very thin but are quite rich in circular muscle fibers; they are lined with a very low epithelium which becomes taller only in the vicinity of the gonopores (Fig. 12, *ovd*).

General Conclusions

I have repeatedly presented arguments in favor of placing the Pogonophora among the Deuterostomia (Ivanov, 1952, 1955b, 1956, 1957). Beklemishev (1944, 1951), Dawydoff (1948), and Jägersten (1956) accept this point of view. Nevertheless the genital apparatus of pogonophores, at first glance, is much more

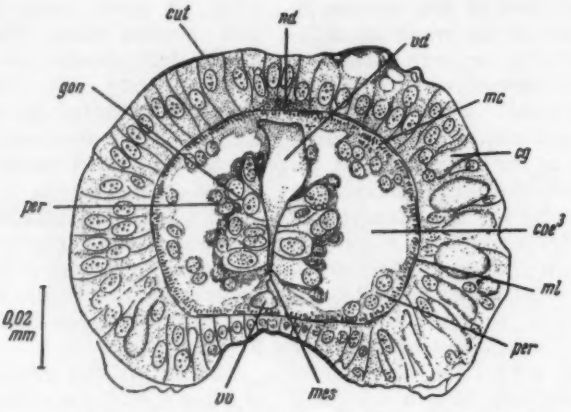

FIG. 10. Transverse section of a young female *Siboglinum caulleryi* posterior to the muscular diaphragm.

like that of the Annelida than of the Deuterostomia.

Actually, in Pogonophora the gonads are closely associated with the coelomic walls and the genital cells occupy a retroperitoneal position. In females the ova are poured into the coelom by rupture of the coelothelial membrane of the ovaries; in males the maturation of the genital cells occurs in the sperm sacs, that is, essentially in the coelom. From the coelom they are emitted by the coelomoducts. The same relationships are characteristic of the annelids.

On the other hand, in the Hemichordata and Acrania, the developed gonads are separated from the common body cavity. However, as is well known, in these ani-

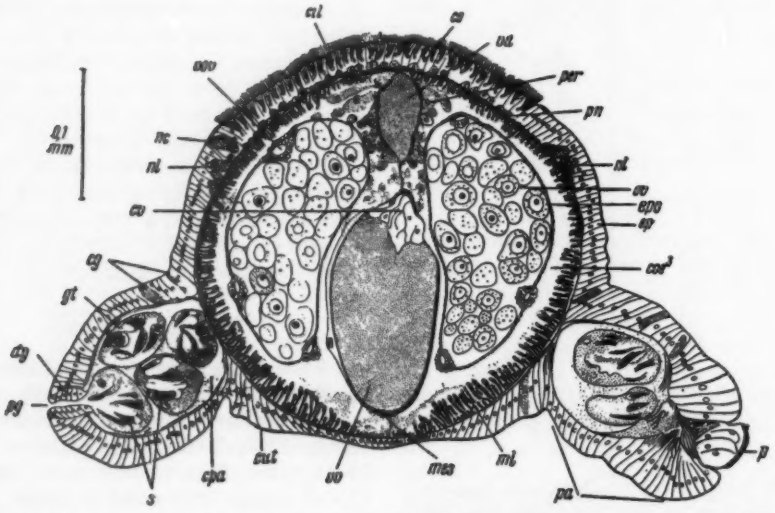

FIG. 11. Transverse section of a female *Polybrachia annulata* in the metameric region of the metasome.

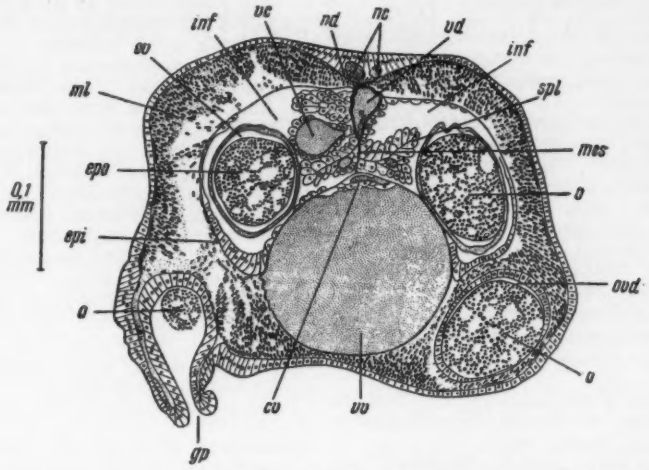

FIG. 12. Transverse section of a female *Polybrachia annulata* at the level of the female gonopores.

mals also the gonocytes appear retroperitoneally, and only later are the gonads specialized from the coelom (Spengel, 1893; Drach, 1948). In the Echinodermata the genital primordium also develops in close association with the coelom. Finally, in vertebrates the gonads are formed on the walls of the common coelomic cavity and the ova are discharged into the coelom. Therefore, there is no difference in principle between the genital apparatus of annelids and deuterostomes in the connection that is of interest to us. Lack of specialization of the gonads from the coelom in Pogonophora is an extremely primitive feature, and in this sense they are formally more closely related to the Annelida than to the Hemichordata, but at the same time they are at the same level as vertebrates. This circumstance is probably explained by the fact that in pogonophores, as in vertebrates, trunk coelomoducts exist through which the genital products are discharged from the coelom.

Therefore, in regard to the phylogenetic relations of Pogonophora, their genital system does not afford any grounds for giving the preference to annelids over deuterostomes.

Explanation of abbreviations on figures

axm, longitudinal torus of spermatic duct; *bc*, ciliated strip of sperm sac; *cg*, gland cell; *cil*, cilia; *co*, dorsal ciliated strip; *coe*^{2}, mesocoel; *coe*^{3}, metacoel; *cpa*, coelom of anchor papilla; *cph*, cytophore; *cr*, crypt of spermatic duct; *cv*, heart; *cut*, cuticle; *dg*, duct of branched tubular gland; *di*, diaphragm; *ep*, epidermis; *epi*, epithelium of coelomoduct infundibulum; *epo*, epithelial wall of ovary; *eps*, epithelium of sperm sac; *fil*, spermatophore filament; *go*, genital papilla; *gon*, oogonia; *gp*, gonopore; *gt*, branched tubular gland; *inf*, infundibulum of coelomoduct; *mb*, basement membrane; *mc*, circular muscle layer; *mes*, mesentery; *ml*, longitudinal muscle layer; *mpa*, muscle fibers of anchor papilla; *my*, myocyte; *nc*, nerve cord; *nd*, dorsal nerve trunk; *nl*, marginal thickening of dorsal nerve plate; *o*, ovum; *ov*, ovary; *ovd*, oviduct; *p*, anchor plate; *pa*, anchor papilla; *per*, peritoneum; *pg*, opening of branched tubular gland; *pn*, dorsal nerve plate; *s*, laminated secretion of branched tubular gland; *smt*, somatopleure; *sp*, sperm cells; *sp*^{1}, *sp*^{2}, *sp*^{3}, stages of spermatogenesis; *spd*, *spd*^{1}, *spd*^{2}, *spd*^{3}, *spd*^{4}, different levels of section of the sperm ducts; *sph*, spermatophore; *spl*, splanchnopleure; *ss*, sperm sacs; *ts*, spongy coelomic tissue; *vc*, transverse blood vessel; *vd*, dorsal vessel; *vov*, ovarian vessel; *vv*, abdominal vessel.

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A. V. IVANOV of the University of Leningrad is continuing his valuable studies on the Pogonophora. His chapter on the Pogonophora has just appeared in the Traité de Zoologie, vol. V, fascicle 2. For reprints of the above article apply to the editor.

Biotic Associations and Extinction

DAVID NICOL

THE ORIGINATION and extinction of animals and plants are continually taking place on the earth, but at least twice since the Cambrian period these processes have occurred, at least among animals, at a greatly accelerated rate. These post-Cambrian faunal revolutions occurred at about the end of the Permian and beginning of the Triassic and again at about the end of the Cretaceous and beginning of the Tertiary. In other words, these two times of relatively rapid extinction and replacement mark the boundaries of the Paleozoic and Mesozoic eras and the Mesozoic and Cenozoic eras. Thus, the study of extinction, besides having historical interest, is fundamental to stratigraphy; indeed, one might ask, "What would stratigraphy be without the occurrence of extinctions among animals and plants?"

The time interval between the two major faunal revolutions is approximately 125 million years, or the duration of the Mesozoic era, but there is no indication that such events occur at regularly spaced intervals.

Some major groups—classes, orders, and families—became extinct at times other than at the end of the Permian and the end of the Cretaceous (for example, the graptolites during the early Mississippian, the conulariids in the late Triassic, and the receptaculitids in the Devonian); but such occurrences were few as compared with those of the two great faunal revolutions. At the Permian-Triassic boundary and again at the Cretaceous-Tertiary boundary the following phenomena occurred: (1) unusually large numbers of major groups became extinct; (2) other major groups rapidly declined to the state of relicts, although in some instances relict representatives remained extant for long periods of time; and (3) during and following these total and partial extinctions, large numbers of other major groups originated.

One of the most puzzling things is that during these faunal revolutions, rapid extinction happened over a wide range of habitats on land and in the water. Simpson, Pittendrigh, and Tiffany (1957:774) refer to the end of the Cretaceous as "The Great Dying" and under this heading make the following observations:

> "Groups that became extinct were of many wholly different kinds living in entirely different environments."
>
> "Other groups living along with them and in the same general environments did not become extinct, and some did not even undergo evident change."
>
> "It is not logically necessary or probable that any *one* factor caused the extinction."

The causes of extinction can be grouped into two classes—physical and biological. No one would deny that these are interrelated, but they are divided here in this way only for the purposes of organization and convenience.

Most writers emphasize the physical causes for the mass extinctions at the end of the Permian and again at the end of the Cretaceous. For example, see Stokes (1960:428–445). Some of the physical causes enumerated by Stokes and others are rapid and widespread orogenies combined with a great amount of volcanic activity which rapidly changed the climate by filling the air with dust and carbon dioxide; an increase of cosmic rays bombarding the earth; the fall of one or more large meteorites which suddenly heated the earth's surface; changes in ocean currents; retreat of epeiric seas; and changes in the positions of the north and south poles, causing climatic zones to shift. Other causes and various combinations of these physical causes could be named.

At the Cretaceous-Tertiary boundary, there is not much evidence within the strata that the physical conditions on the earth were exceptionally severe. This does not mean that severe or unusual physical conditions did not occur at the end of the Cretaceous period, but the evidence in the rocks of such conditions is meager. This is not true of the strata around the Permian-Triassic boundary, which commonly indicate widespread aridity and drying up of the epeiric seas. However, since the Cambrian there have been other periods of extensive severe climatic conditions which were not coupled with unusually widespread or rapid extinction of many groups of animals.

The biological causes, on the other hand, have not been considered by most writers in the same amount of detail as the physical causes. In a few instances, overspecialization and racial senescence in certain groups of organisms have been postulated and discussed at some length, but other biological factors perhaps leading to mass extinction have generally been summarily handled. One of these, the ecological associations of organisms, has commonly been completely neglected. An exception to this statement is found in an interesting book by Beerbower, *Search for the past*, in which he alludes to this phenomenon in the following passage (1960:183):

> "If, as seems possible, adaptive relations are the result of complex ecosystem evolution, the species produced by the radiation are in rather delicate ecologic adjustment to one another. If someone upsets the applecart by becoming extinct—due, say, to climatic change —the whole system is likely to be unfavorably affected. What paleontologists need is precise analysis of faunal assemblages before and during a wave of extinction—not metaphors."

Some workers have also mentioned the adverse effect of the predominately angiosperm vegetation on the terrestrial dinosaurs as a cause for their rapid extinction at the end of the Cretaceous. Finally, the possibility that mammals ate dinosaur eggs, thus hastening the extinction of these reptiles, has been suggested by some paleontologists.

The ecological associations of organisms and how these associations may affect extinction should, I believe, be further explored. My discussion of this theme will of necessity be limited mainly to the fauna with which I am most familiar, viz., marine mollusks of the late Cretaceous and early Tertiary. The span of time in question was probably no more than 10 million years, but the changes in much of the marine molluscan fauna during that geologically brief time were great.

Before reviewing the history of the mollusks at the end of the Cretaceous, perhaps it would be apropos here to mention a few ecological relationships. Different kinds of organisms are intimately associated in nature, and some of these associations are symbiosis, commensalism, and parasitism. In general, one free-living species provides an ecological niche for one or more symbionts, commensals, or parasites. If the free-living species becomes extinct, then one or more of its associated symbionts, commensals, or parasites may become extinct because they cannot associate quickly enough with another species or become accustomed to some other host. Another relationship that must be considered is that of competition between two or more different groups of animals for the same kind of food or living space. The higher the taxonomic rank of the competing groups (e.g., classes or phyla instead of genera or species), the more generalized the competition is likely to be; nevertheless, if the competition is between, let us say, two groups of filter-feeders such as most of the pelecypods and brachiopods, one of the competing groups may diminish much more extensively than the other. Furthermore, even without competition from another group, a consumer may be starved to extinction if any phenomenon, biological or physical, reduces its food supply. In other words, the ecologic balance of a community of animals can be upset by having something happen to one of the members of a food pyramid. If one of the lower members of the food pyramid disap-

pears or perhaps even becomes scarce, this may upset all the other groups above it, possibly causing the extinction of several major groups of animals. The only escape for these higher members of the food pyramid is to utilize another food organism; this is sometimes impossible. See Simpson, Pittendrigh, and Tiffany (1957: 620–624) and Allee et al. (1949:522–528) for discussions of food pyramids and pyramids of mass and numbers.

Little is known about competition between groups of organisms in the past. That it occurred, however, is indicated by the Mesozoic history of the cephalopods, particularly the ammonoids and nautiloids. Whenever one of these two groups expanded in numbers of genera, the other invariably declined; and it is interesting to note that the situation between them was reversed at least twice after the end of the Permian. Simpson, Pittendrigh, and Tiffany (1957:774) observe:

"The late Cretaceous was a time of widespread extinction. Among the many invertebrate groups that declined or died then, the ammonites are most striking. They are extremely abundant in most Cretaceous marine rocks, but near the end of that period they disappeared completely and for good. It is interesting that they had *almost* become extinct long before, at the end of the Triassic, when only one small group, probably only a single genus, survived. From it, however, a tremendous new radiation occurred in the Jurassic and into the Cretaceous. The failure of even one genus to pull through the similar crisis at the end of the Cretaceous and to restock Cenozoic seas may have been due to competition from then abundant squidlike cephalopods—but that is speculative."

Miller (1949:231) points out that the nautiloids were flourishing in the late Triassic during the time that the ammonoids nearly became extinct. Subsequently, during the Jurassic and Cretaceous, when ammonoid genera became numerous, the nautiloids declined. Miller (1949:232) states:

"Although it does not appear to have been emphasized previously, it now seems likely that the nautiloids almost became extinct at the close of the Mesozoic, and only one genus, *Eutrephoceras*, is definitely known to cross into the Cenozoic. It is a more or less generalized type characterized by a globular conch and almost straight external sutures, and it is the only nautiloid genus that was abundant and widespread during the Upper Cretaceous."

Finally, the situation was reversed once more, and Miller reports (1949:231–232):

"Near the end of the Cretaceous, the ammonoids, like many other kinds of animals, suddenly became extinct, and their disappearance gave the nautiloids a new lease on life."

With ammonoid competition eliminated, the nautiloids flourished in the early Tertiary.

An interesting question naturally arises here. Would the nautiloids have become extinct sometime in the early Tertiary if the ammonoids had not become extinct at the end of the Cretaceous period?

In each of the reversals, which was the cause and which the effect? Near the end of the Triassic, as has been stated earlier, the ammonoids seemed to be approaching extinction and the nautiloids were expanding. At that time, did the decline of the ammonoids, caused by unknown factors, give the nautiloids a chance to increase greatly in numbers of genera and species, or did the ammonoids decrease because of the growing pressure and competition from newly developing genera and species of nautiloids? The former alternative is the more likely in view of the fact that later, at the Cretaceous-Tertiary boundary, the nautiloids did not increase in numbers of genera until after the ammonoids had become extinct. Generally the replacing group does not expand a great deal as to numbers of genera until the competing group has become extinct. This is true of the ammonoids and nautiloids and also of the dinosaurs and mammals.

At the end of the Cretaceous, why did extinction befall the ammonoids instead of the much less numerous nautiloids? Heretofore, the proposed answers to this puzzling question have generally been that the ammonoids were overspecialized

and also more racially senescent than the nautiloids. The latter idea is based on two things—the more complex suture pattern of the ammonoids and the fact that several genera of late Cretaceous ammonoids showed some bizarre kinds of coiling whereas the nautiloids were all planispirally coiled at that time. In many cases racial senescence is difficult to prove on the basis of morphological characters alone. For example, the complex suture pattern was present even when the ammonoids were expanding dynamically. If the ammonoids became senescent at all, their senescence was most likely a biochemical matter affecting the genes and chromosomes and was not necessarily apparent in the morphological characters of the shell. Overspecialization, too, is difficult, if not impossible, to prove. Certainly the brachiopod *Lingula* is specialized to a rather limited environment, but it has been eking out an existence for at least 400 million years.

Ecological factors may have contributed significantly to the extinction of the ammonoids before the nautiloids. That the late Cretaceous ammonoids had predatory enemies has been proved by Kauffman and Kesling (1960) in their excellent study of a specimen which bears clear evidence of having been bitten and eaten by a mosasaur. According to Kauffman and Kesling (1960:235):

> ". . . The mosasaur was in the habit of eating ammonites. The plan of assault—seizure from above, attempt to swallow whole, and failing this, crushing the living chamber to squeeze out the soft parts—seems to indicate familiarity with the prey. The large, conical, biting teeth and the wide intermaxillary angle appear to be adaptations for catching, killing, and swallowing or crushing big-shelled animals, such as ammonites."
>
> "The mosasaur was most likely a deep diver of the Platecarpinae, a close relative of *Platecarpus brachycephalus* and *Ancylocentrum overtoni*, and a feeder on large cephalopods."

Thus, perhaps the ammonoids were one step below some of the mosasaurs in a food pyramid; and when the mosasaurs eliminated their favorite food they may have caused their own extinction, for the mosasaurs disappeared along with the ammonoids at the end of the Cretaceous. Mosasaurs may also have been an important factor in the near elimination of the belemnoids at the end of the Cretaceous. More detailed ecological observations of the type done by Kauffman and Kesling are needed to help solve the many problems of extinction of certain groups of animals.

The rapid expansion of the modern teleost fish families during the late Cretaceous may have been another factor in the extinction of first the ammonoids and shortly thereafter the belemnoids. Certain large teleosteans may have found the cephalopods a common and easy prey.

The very fact that the ammonoids were more numerous than the nautiloids may have led to their extinction because they had more enemies. In other words, a certain amount of success begets more enemies. Perhaps, also, this predator–and–prey association explains the numerous relicts or "living fossils." These relicts, in some cases comprising only one surviving species of a formerly large group, continue to eke out an existence for a relatively long time because most or all of their natural enemies are either extinct or have turned to other, more abundant animals on which to prey. These are but a few simple illustrations; in most cases the associations were probably more complex and involved more than two groups of organisms. Nevertheless, these possibilities should not be overlooked by paleontologists and biologists in their search for the causes of total and partial extinctions.

The fact remains that the nautiloids replaced the ammonoids for a time in the early Tertiary. It took the nautiloids probably no more than five million years (the early Paleocene) to culminate their rapid expansion in numbers of new genera after the disappearance of the ammonoids. After the Paleocene, the nautiloids once again declined in numbers of genera and

species, and today they are a relict group confined to a relatively small part of the Pacific Ocean. Probably linked with the disappearance of the ammonoids and the rise of the nautiloids was the almost total disappearance of another cephalopod group, the belemnoids, at the end of the Cretaceous. Another factor contributing to the decline of the more primitive cephalopods may have been the origination of modern cephalopods, the various groups of existing coeloids which arose in the Jurassic and Cretaceous. This possibility was previously pointed out by Simpson, Pittendrigh, and Tiffany. As the more progressive groups like the sepioids, teuthoids, octopods, and teleost fish attained a certain abundance, one after another of the more primitive groups was pressed toward extinction. The extinction of each group in turn may have led to the extinction of another; and once the ecologic balance was upset, the faunal changes could occur with startling suddenness.

The pelecypods underwent many changes, too. The rudistids became extinct during the early Paleocene. Among the Ostreidae the abundantly represented genus *Exogyra* disappeared and the gryphaeoids became rare at the end of the Cretaceous. Another ostreid stock, *Arctostrea,* and its relatives also disappeared at the end of the Cretaceous, and there was a general diminution of the variable ostreid forms at the end of the Mesozoic era. Other filibranchs, such as *Oxytoma, Inoceramus,* and *Gervilleia,* were also casualties at the end of the Cretaceous. The pectinoids underwent several changes. *Neithea, Camptonectes,* and *Syncyclonema* were replaced in the Tertiary by more modern forms. The Cucullaeidae and Trigoniidae underwent drastic reduction and are now only Indo-Pacific relicts. The abundant and varied Mesozoic desmodonts also almost completely disappeared. *Goniomya, Cercomya, Homomya, Arcomya,* and *Flabellomya* became extinct as the Cretaceous period drew to a close, and *Pholadomya* gradually declined and is today a deep-water relict. Perhaps the competition from the rapidly developing tellinids and venerids, particularly the former group, forced the Mesozoic desmodonts toward extinction. The irregular echinoids may have competed with the desmodonts for living space on the soft substrate. The skates and rays among the sharks, which became abundant in the late Cretaceous, may have taken their toll of the more primitive burrowing pelecypods. Many more groups of pelecypods, such as *Arctica, Fimbria,* and *Glossus,* rapidly waned at that time and are today represented by few species in limited geographic areas. The overall picture of the pelecypods is one of great change at the Mesozoic-Cenozoic boundary, but there is no indication of a reduction of numbers of families, genera, and species during the Tertiary period. Replacement among the pelecypod families and genera, however, is common. For example, the chamids probably took over some of the ecologic niches in the Tertiary formerly occupied by the rudistids in the Cretaceous.

The gastropods tell an entirely different story. Although they increased greatly in variety as the end of the Cretaceous approached, the origination of new families and genera was not commonly accompanied by the extinction of others. Except for some late Cretaceous endemic forms, only the nerineids, *Anchura,* and possibly *Gyrodes,* were eliminated. Most of the common Mesozoic gastropods still survive, although quite a few groups have waned since the Mesozoic era and are now relicts.

In summary, the Mesozoic and Cenozoic history of the three important classes of mollusks indicates three different patterns of extinction and replacement. Many cephalopod families and genera became extinct but very few new ones are known to have arisen in their place. The lack of recorded replacement may be at least partly due to the fact that the more advanced cephalopods, such as the modern

coleoids, have little or no skeletal material and are therefore less likely to be preserved for the fossil record. The pelecypod groups showed a considerable amount of extinction but were replaced by others; some of this replacement started before the end of the Cretaceous. There was probably no net reduction of numbers of pelecypod families, genera, and species, nor is there any indication of a net increase, at the Cretaceous-Tertiary boundary. Comparatively little extinction is shown among the gastropods; and starting with the late Cretaceous, the gastropods increased greatly in numbers of families, genera, and species.

One further comment on the decline of the cephalopods should be interjected here. Throughout the Mesozoic and continuing to the present time, the families, genera, and species of the class have probably always been less numerous than the marine representatives of the pelecypods and gastropods. In proportion to their numbers, the decline of the cephalopods at the end of the Cretaceous may have been extensive; but because the numbers were comparatively small to begin with, the losses were probably fewer than has commonly been supposed. The likelihood that the cephalopods were a relatively small group is based on two premises: (1) All cephalopods are and probably were active and predatory or carnivorous animals. Because predators commonly prey on more than one kind of victim, they are generally less varied and numerous as to genera, species, and individuals than are animals which stand lower on the food pyramid, as certainly most pelecypods and gastropods do. (2) Furthermore, modern cephalopods have a smaller variety of food habits and occupy less diverse habitats than do the marine gastropods and pelecypods. Morphological and paleoecological evidence indicates that this was also true in the past.

Why one class should increase greatly in variety, another remain about the same, and a third decline at the end of the Cretaceous is difficult to explain. However, this same phenomenon can be shown to have occurred also among some of the other principal invertebrate groups and among the vertebrates at the end of the Cretaceous period. In general, those major groups that lost many of their genera and species at the end of the Cretaceous became further reduced or failed to rally during the Tertiary. Those groups that underwent little extinction at the end of the Cretaceous (gastropods and teleost fishes) generally increased in numbers of genera and species during the Tertiary period.

It has been noted in the paleontologic record that great increase in the body size of individuals is usually soon followed by extinction of the group. For example, in the late Cretaceous, some of the ammonoids, rudistids, and *Inoceramus* attained large size. One possible explanation for this close connection between gigantism and extinction is that as the individuals of an animal group increase in size they necessarily must have more area in which to live and gather food. This would naturally tend to reduce the number of large individuals living in an area—tend to reduce the size of local populations. If these populations were reduced enough so that the number of matings was reduced, resulting in a decline of the birth/death ratio, gigantism would probably lead to extinction of the group. Food habits, mobility, and mode of reproduction would all be factors in determining what maximum size the individual animals could attain before local populations would become so attenuated as to lead to extinction.

The intimate relationship of stratigraphy and paleoecology with extinction should be further explored. If more information were brought to light concerning the habits and habitats of animals that lived in the past as well as today, and if ecologically associated groups—for example, pelecypods and brachiopods—were carefully enumerated as to the numbers of genera and species existing before, during, and after a wave of extinction, then

we might better understand the geologic histories of the groups which competed with each other for food or living space.

Acknowledgment

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Points of View

Biological Species and Phylogenetic Taxonomy

We agree with most of the points made by George Myers (1960) in his reflections on "phylogenetic" versus "typological taxonomy" but are impelled to take strong issue with him on the application of "biological" information in the classification of species. Myers' defeatist attitude that such information should not be used because this kind of information is not available for all species is a puzzling position for a scientist to take. The argument is simply that we should not correctly classify organisms where we have adequate evidence because we cannot correctly classify all organisms. By extension of this position, we can visualize the state of systematic biology if Linnaeus and other pioneers had been able to foresee the diversity of organisms that would ultimately become known to science and, therefore, had refrained from classifying the organisms they knew simply because they had a defeatist attitude toward the possibility of classifying this array of organisms in the foreseeable future.

Myers' position of objecting to "biological species based on interbreeding potential," seems to us to result from his misinterpretation of Mayr's (1942) usage of "interbreeding potential." Myers states "Moreover, evidence is accumulating that the interbreeding situation in birds, upon which Mayr's ideas were based, is not necessarily typical of other groups of animals. In fishes, interordinal hybrid larvae can be produced, and apparently some morphologically and behaviorally distinctive species happen to be easily hybridized in the laboratory (and produce fertile hybrids) but nevertheless maintain complete genetic isolation in the field, even when existing in the same habitat." This implies that Mayr would consider that the capacity to produce hybrids is evidence of conspecific relationship. Mayr actually states (p. 119) ". . . the criterion of fertility is part of many modern species definitions. 'All forms belong to one species which can produce fertile hybrids.' Unfortunately, this statement is not at all true, there being numerous cases known in which good species have freely produced completely fertile hybrids. . . ." Mayr knew that valid natural species could produce hybrids under laboratory conditions. Moreover, Mayr did not base his conclusions exclusively on birds, for he cited evidence on a wide diversity of animals from *Paramacium* to insects and mammals as well as plants. A growing literature too extensive to be cited here shows that similar generalizations about the nature of biological species can be drawn from a diversity of additional organisms.

There are essentially no well-informed students of biological species who are unaware of the fact that closely related species frequently prove fertile in the laboratory; in the groups with which we work this is the common order of things and deviations from it are the exception. The critical evolutionary acquisition of a population is the development of an effective set of isolating mechanisms that functions in natural environments. Genetic incompatibility may or may not be a part of the complex of isolating mechanisms in any particular instance.

Myers' use of "known interordinal hybrids" in fishes as an argument against hybridization as a major criterion of spe-

cies relationship is not germane because those hybrids die just after hatching. The valid interordinal hybrids are between species of *Menidia* and *Fundulus heteroclitus* whereas the other "interordinal hybrids" are gynogenetic. The validity of these hybrids is substantiated by other interordinal hybrids between *Menidia beryllina* ♀ and *Fundulus pulverus* ♂ and *F. grandis* ♂. Such data can be explained alternatively by considering that hybrids can be produced between distantly related orders or by questioning the validity of the orders. The latter was done by Hubbs and Drewry (1960) who supported Myers' (1928) suggestion of close relationship of the two groups.

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A Cyclical Evolutionary Process

Evolution is a dynamic process and, in general, may be looked upon as responses of organisms to changes in ecological niches, either through nonorganic (e.g. geological) processes, or through the interplay of the selective forces caused by the organisms themselves. Thus the generalization can be made that if environmental changes were to cease, evolution would eventually cease. In addition, evolution generally leads to organisms which are more and more efficient in coping with their environment as more successful species eliminate the less successful ones. It therefore seems desirable to call attention to a situation which, at least in theory, could lead to a cyclical evolutionary process through little or no pressure from environmental changes and which would see a succession of species which would not necessarily differ in their fitness with respect to their environment.

Recently Eberly (1960) has described an interesting situation which obtains between two species of crayfish living in Indiana caves. The reader is referred to the original article for details of the relationship but the following data are most pertinent for this discussion:

1. *Orconectes pellucidus* appears to have been cavernicolous for a longer period and consequently is better adapted to cave life than *Cambarus bartoni* as shown by:

   a. complete loss of pigment.
   b. loss of function of eyes.
   c. increased tactile sensitivity.
   d. lower metabolic rate.
   e. a more attenuated and less robust build.[1]

The first three features are related to the absence of light from caves while the latter two are adaptations to a decreased food supply.

2. Populations of *Cambarus bartoni* which live in caves seem to be evolving towards increased cave adaptation (especially with respect to tactile sensitivity) but are poorly adjusted to the small supply of food as evidenced by the starvation

[1] Although Eberly's conclusions as to size relationships and oxygen consumption are herein accepted, it is suggested that the weight-length data are more informative if presented as the ratio W/L^3, which is dimensionally better suited as an index of stockiness (the values for the data given are .020, .018; and .031, .037 g/cm^3, for *Orconectes* and *Cambarus*, respectively.) With respect to oxygen consumption, it would seem that the oxygen consumed per individual would be a more reliable index of the ability of a species to survive on a minimal supply of food.

to which these populations are apparently susceptible.

3. Thus in isolated populations, *Orconectes pellucidus* is the better adapted and more successful species and on this basis should survive any competition between the two forms.

4. However, one of the very factors which makes *Cambarus bartoni* relatively poorly adapted to cave life, i.e. its "robustness" (used here to mean both greater physical size and greater activity), enables it to overcome and prey upon *Orconectes*. Thus *Cambarus* not only competes with *Orconectes* for food, but also preys upon the latter. In populations containing both species, *Cambarus* may be expected to cause the extinction of *Orconectes* unless the latter adapts to a special niche. This has possibly occurred already in those areas where a species of *Cambarus* but none of *Orconectes* is known.

If Eberly's propositions are correct,[2] we should see the following evolutionary events:

1. *Orconectes* (A) is replaced by *Cambarus* (B) by virtue of the physical superiority of the latter. After the extinction of *Orconectes*, the population level of *Cambarus* probably would be rather drastically reduced because of the reduction in food supply.

2. As soon as the interspecific competition (between A and B) is removed by the extinction of A, B will, through intraspecific competition, become better and better cave adapted, i.e. it will probably become more and more like the previously existing A.

3. At some point it will be possible for another epigean form (C), although poorly cave-adapted, to compete successfully with B and eventually replace it by virtue of its greater robustness.

As can be seen, stage 3 is identical with stage 1 and we have a cyclical process alternating between 1) competition between two species and 2) adaptation of a solitary species to its environment. The only condition (other than those leading to cave-adaptation) which is necessary for the above situation is some mechanism whereby in stage 2, the epigean and hypogean populations of B can speciate and prevent gene exchange. This could most readily be accomplished *via* spatial separation of the incipient species; although perhaps this is not necessary. Any mechanism resulting in incompatibility would be favored even if complete spatial separation were absent, since it would prevent the exchange of poorly adapted genes from one population to the other. Thus the two forms could be parapatric and still diverge if selection were more important than migration (see Dobzhansky, 1951).

Thus we have a cyclical process hinging upon a given trait (robustness) the fitness of which varies widely depending upon whether the major competition occurring is inter- or intraspecific. The fact that a solitary species tends to become more and more "fragile," ending in its extinction by a more robust species, may seem to carry implications of orthogenesis, but simply results from the constant selective pressure of food supply interacting with the variable, but at times more intense, selective pressure of a robust competitor and predator.

This type of situation in which one finds a series of species A,B,C, . . . occurring with the passage of time should not be confused with the common zoogeographical situation wherein a series of species A,B,C, . . . occurs through dispersal of waves of species, each of increased fitness, i.e. ${}^{w}C > {}^{w}B > {}^{w}A$. In the present situation, at least in theory, it is possible that the fitness of each species (at corresponding stages in the cycle) may be the same, i.e. ${}^{w}A = {}^{w}B = {}^{w}C$. . . .

This situation, though uncommon, should not necessarily be unique. Any

[2] Discussions of this subject with associates have raised questions as to the validity of some of Eberly's conclusions. However, this has no direct bearing on the discussion at hand inasmuch as it is the *model* which is central to the discussion rather than the particular situation obtaining in Indiana caves.

area having strong selective pressures arising from the environment rather than competitors and at least partially isolated from an adjacent area of different environment might be expected to exhibit a similar situation. An example would be a semi-isolated island which is populated only by chance immigrants. Lacking interspecific competition, a form could become so well adapted to the non-organic environment (at the expense of other traits) that upon the arrival of a competitor, it would become extinct and the cycle could then start over. In general, one can say that environments in narrow adaptive zones wherein the biotic and the physical selective pressures are antagonistic, and which are semi-isolated from nearby environments with widely diverse pressures, are conducive to cyclical evolutionary processes.

The views presented here are, of necessity, speculative in that the subject does not lend itself readily to either experimental or theoretical investigations. Nevertheless, they suggest that careful investigation of the situations described above might lead to evidence supporting cyclical processes.

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The Order Pharetronida in Hartman's Classification of the Calcarea

Hartman (1958) has published a revision of Bidder's (1898) classification of the Calcarea in the light of all embryological and anatomical observations made since that date. These new data confirm the subdivision of the Calcarea into two subclasses, the Calcaronea and the Calcinea, as suggested by Bidder on the basis of the position of the nucleus in the choanocytes and of features of the larvae. In calcinean sponges the choanocytes have basal nuclei with flagella arising independently of the nuclei; parenchymula larvae are present. In calcaronean sponges the choanocyte nuclei are apical with flagella arising from them directly, and amphiblastula larvae are present. Certain characteristics of the spicules serve to emphasize this subdivision, especially the triradiates which are equiangular in the Calcinea and sagittal and inequiangular in the Calcaronea.

Hartman's classification, inspired by the work of Bidder, seems a very satisfactory one except for the Pharetronida, an order which poses problems difficult to resolve on account of the scarcity of these sponges and the little we know about them.

Previously Dendy and Row (1913) assumed the order Pharetronida, composed of three families, to be a diphyletic one. Indeed, only the family Lelapiidae has choanocytes with apical nuclei; the Minchinellidae and Murrayonidae have basal choanocyte nuclei. This fact led Hartman to place the order Pharetronida, restricted to the last two families, in the Calcinea; the family Lelapiidae, excluded from this order, is placed in the Calcaronea.

The study of a Mediterranean pharetronid, *Petrobiona massiliana* Vacelet and Lévi, 1958, placed, perhaps temporarily, in the Murrayonidae, brings to light some data which complicate this problem. The anatomy and skeleton of this sponge are typical of the Murrayonidae, but the choanocytes (Fig. 1) are leucosolenid, with an apical, pear-shaped nucleus, 3 μ in diameter, with the flagellum arising directly from the nucleus. The choanocytes measure 5 to 7 μ in diameter. The larvae

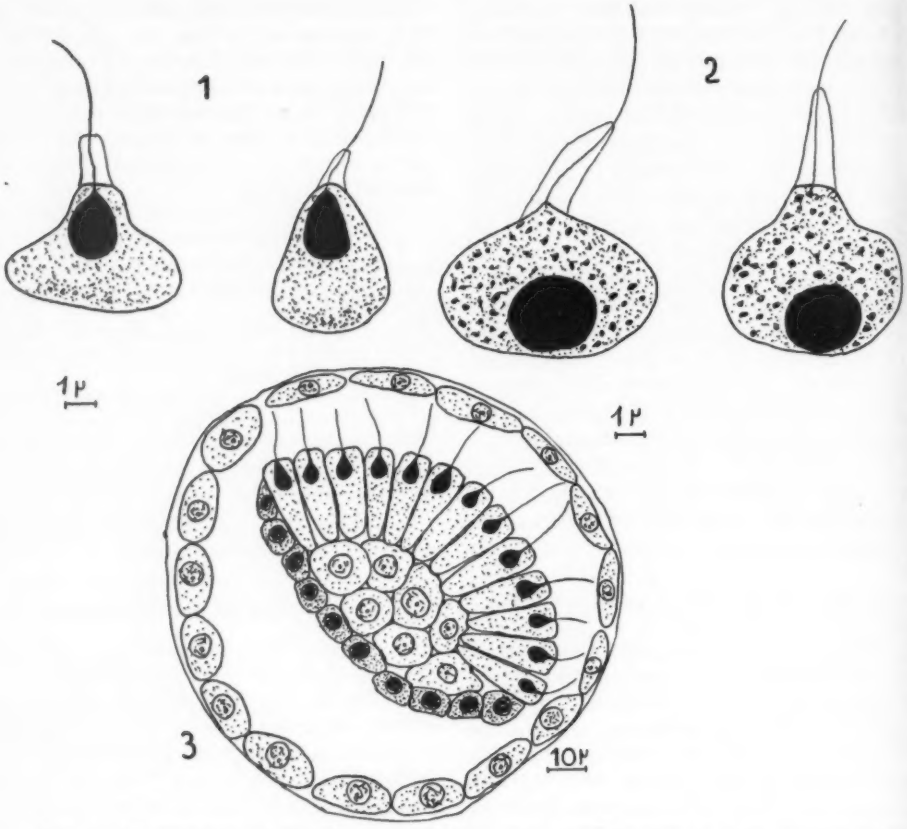

FIG. 1. Choanocytes of *Petrobiona massiliana*. FIG. 2. Choanocytes of *Murrayona phanolepis*. FIG. 3. Larva of *Petrobiona massiliana*.

(Fig. 3) are typical amphiblastulae. The triradiate spicules are sagittal and inequiangular. This sponge is a calcaronean, therefore.

These data oppose *Petrobiona massiliana* to the single other known representative of the family Murrayonidae, *Murrayona phanolepis*. Kirkpatrick, who described this sponge in 1910, did not give details on histology because fixation and preservation had not been carried out properly. Dendy and Row (1913), after examining Kirkpatrick's sections, concluded that the choanocyte nuclei are basal in position. Through the kindness of Miss S. M. Stone of the British Museum (Natural History) I have been able to compare these slides of *Murrayona* with my sections of *Petrobiona*. The choanocytes are certainly different in the two genera. In *Murrayona phanolepis* the choanocytes (Fig. 2) are conical cells, 6.5–8.5 μ in diameter, with a spherical nucleus (3.5–4.0 μ) located basally. Collar and flagellum are often visible. In some of these cells the flagellum seems to arise from a small black point which may be the blepharoplast, but the slides are not good enough to be certain about this question. The choanocytes of *Murrayona* are quite similar to those of *Petrobiona*, but the position of the nuclei is opposed. Other characteristics of the two sponges are very near. The calcareous central

skeleton of *Petrobiona* is made of less regular bodies and is more compact; *Murrayona* has calcareous scales which are lacking in *Petrobiona*. These points are not very important. Larvae of *Murrayona* are not yet known, but the triradiates are sagittal and thus characteristic of the Calcaronea. The central skeleton of the two genera is so peculiar among calcareous sponges that it seems rather difficult to put them into different subclasses on the basis of the location of the choanocyte nuclei.

Another puzzling pharetronid sponge is *Minchinella lamellosa* Kirkpatrick, the only representative of the Minchinellidae the histological features of which have been well described. Kirkpatrick (1908) states, "The collar cells are large, with a flattened body containing a very large nucleus nearly filling the cell . . .; the base has a circular outline and the nucleus is always seen at the side of the cell. . . . The flagellum is clearly visible outside the collar, but I could not trace it down inside. Prof. Minchin, to whom I showed the sections, considered that the collar cells had a 'Leucosolenid' rather than a 'Clathrinid' aspect; . . . It may be mentioned here, too, that the sagittal spicules of *Minchinella* suggest Leucosolenid affinities." *Minchinella lamellosa*, in spite of the peculiar aspect of the choanocytes, would be placed in the subclass Calcaronea; its nonamoeboid spermatozoans are in favor of this (but this characteristic is based only on *Clathrina, Leucosolenia*, and *Sycon*). The larvae, observed by Kirkpatrick, are parenchymulae, however, a calcinean characteristic.

Lastly, tuning-fork triradiates, very common among fossil pharetronids, are found in all three existing families of the order. Only two other species of Calcarea (*Leucandra pulvinar* Haeckel and *L. pandora* Haeckel) have this type of spicule.

In summary, the following table may be constructed:

	Nucleus of choanocyte	Larva	Triradiates
Leucosolenia	Apical	Amphiblastula	Sagittal
Clathrina	*Basal*	*Parenchymula*	*Equiangular*
Lelapiidae	Apical	?	Sagittal
Petrobiona	Apical	Amphiblastula	Sagittal
Murrayona	*Basal*	?	Sagittal
Minchinella	(?) Filling the cell	*Parenchymula*	Sagittal

Calcinean characteristics are in italics.

In conclusion, *Petrobiona massiliana* and the Lelapiidae may surely be placed in the subclass Calcaronea. *Murrayona phanolepis* has one feature of the Calcinea, another of the Calcaronea; larvae are unhappily unknown. Moreover, the skeleton of *Murrayona* resembles that of *Petrobiona*. Likewise *Minchinella lamellosa* shows features of the two subclasses: calcinean larvae, but calcaronean triradiates and peculiar choanocytes difficult to classify.

This mixture of characteristics, added to the common points of all these sponges, are in disagreement with Hartman's classification.

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